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THE HOROKIWI STREAM

A STUDY OF A TROUT POPULATION

by

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PART I

Introduction

1. OBJECTS

It has long been realized that the amount of food available may have an important effect in determining the number, rate of growth and other characteristics of the trout population in any particular water. This possibility has been recognized in those fisheries management practices which are aimed at adjusting the numerical density of a trout stock in accordance with the food supply. Thus, in some widely-used stocking tables (Embody, 1927), the number of fish to be introduced into unit length of a stream of given size is varied in accordance with the "food-grade" of the stream. The "food-grade" is determined from the overall density of all forms in the bottom fauna, and three categories of streams are recognized.

Such practices have, however, largely been based on general impressions as to suitable stocking densities, and their tentative nature has been emphasized by Embody himself, and by Davis (1938) who stated that the recommendations "are purely tentative and will doubtless require considerable revision in the light of future investigations." A great deal of data regarding the feeding habits, growth rates, and spawning habits of trout and other fish has been amassed, but in most cases the results are largely qualitative and have been little collated with the environment inhabited by the fish. In some instances, quantitative measurements have been made of either the standing stock or the yield to anglers for a particular fish population, but the data are rarely sufficiently comprehensive to allow of an effective study of the actual food requirements of the population, the method in which it is utilized and its influence on the ultimate yield to the angler.

Thus, while most of the factors necessary to a quantitative study of the relation between a trout population, its food supply, and the yield to anglers have been separately studied in isolated instances, it does not appear that all the problems involved have been examined and collated for a single population of trout, or indeed of any other fish. As the problem is essentially a quantitative one, it seems essential for any satisfactory advance that as many as possible of the significant quantities should be observed for the same population over the same period. Therefore, when an opportunity arose in 1939 to start a new long-term research programme, it was decided to attempt a comprehensive quantitative study of a small isolated trout population, the factors by which it was controlled, and, particularly, its relation to its food supply. The resources available for the work were strictly limited in that the whole programme had to be carried out by one scientist, with a single assistant for the field work. It was realized that if the objects of the investigation were to be attained a considerable quantity of carefully co-ordinated

data would have to be collected simultaneously, and that the final details of the programme could only be worked out as the work developed, and actual experience showed how much could be accomplished with the resources available.

The whole study was therefore regarded not only as an attempt to obtain data regarding trout population dynamics, but also to an even greater extent as an experiment in technique, which was aimed at determining what data were required, and how they could be most economically obtained. In order to extract the maximum benefit from this aspect of the study, much attention has been paid in the analysis of the results to the estimation of the probable errors of the various determinations. In this way it was hoped to ascertain whether the results were sufficiently reliable to justify the effort involved, and also which sections of the programme would particularly repay the development of improved techniques in any repetition or extension of the work.

Field work on the programme began in February, 1939, and was continued until October, 1941, when war conditions brought the work to an enforced halt. A preliminary account of the work and a general outline of the results have been published earlier (Allen, 1946), but when that account was prepared time had not permitted detailed statistical analysis of the data. In the more complete account which follows some of the estimates differ from those published earlier, but not sufficiently to have a significant effect on the relationships between the various quantities studied.

In addition to the quantitative results regarding the trout population and its food supply, as much information as possible has been presented regarding the general background, both historical and physical, of the population studied. It is apparent that at the present time we have not sufficient knowledge of the factors affecting fish stocks under natural conditions to be sure which are of importance. The background data have therefore been presented in the hope that, although not directly relevant to the present study, they may be of value in comparing the results obtained in this work with those of other similar studies.

2. PROCEDURE

The principle of an investigation into the relation between a fish stock and its food supply appeared to be to follow the trout population over a period, observing the number, growth, age and distribution of all year-classes present, and at the same time to obtain as accurate an estimate as possible of its food supply, including any fluctuations. With such data it should be possible to examine the relation between the size of the population, the growth of the individuals, the amount of food eaten and the food supply available. If the angling yield from the population studied were also measured, it should be possible to correlate this with the amount of trout being produced.

It was apparent that the estimation both of the fish population and of the food supply had to be based on sampling methods. It was therefore necessary to carry out a physical survey of the whole of the water system concerned, in order that the areas sampled could be used as a basis for the calculation of complete popula-

tions. This survey had to show not only the length and area of the stream but also the area of each type of water (pool, run, etc.) and also the area occupied by each type of bed (shingle, sand, etc.).

The most practicable means of determining the size and composition of the entire trout population appeared to be to take a periodic census of selected representative areas, and to compute the total population from the census data by using the results of the physical survey. Since it might become necessary to divide the stream into a number of regions, it was essential to have the data in such a form that the various quantities could be easily determined for any desired section of the stream. The census of the sample areas would be best carried out by collecting the trout within each area as completely as possible, and by applying a correction determined by further studies for the probable number of fish missed. It is obvious that the accuracy of the estimate will increase with the size and number of the sample areas. These, as well as the frequency with which a census can be taken, are limited by the amount of time which can be devoted to this phase of the work, and any scheme of observations has to be a compromise in this respect. The data on sizes and growth rates and on stomach contents could be obtained to some extent from the fish collected during the census work, but it might be necessary to take additional collections at more frequent intervals for this purpose. In the removal of fish for the study of stomach contents, a further compromise is involved between the number which it would be desirable to kill to obtain reliable data, and the number which may be taken without unduly affecting the population; this conflict may become serious among the older age-groups, which may be few in actual numbers in a small stream.

Since the trout studied were found to feed almost entirely upon the bottom fauna, the estimation of food supply involved the estimation of the bottom fauna. This is most effectively carried out by taking, at regular intervals, a series of quantitative collections with some sampling device. The series of collections must conform to a pattern which will ensure that sufficient data are available for all stream and bed types in all regions to enable an estimate of the entire population to be made with the aid of the physical survey data. Here again a compromise becomes necessary between the number and frequency of collections which are desirable for accuracy and the number which can be made in the time available.

3. SELECTION OF AREA

When the work was being planned the following features were listed as essential in any stream selected as a site for this study.

(i) Suitable size. In order to make the investigations as complete and thorough as possible, the stream should be no larger than is necessary to provide an adequate quantity of trout. A total length of 7 to 10 miles seems to be indicated.

(ii) A minimum of tributaries and forks, since the less a stream branches the greater the proportion of the total length of waterway which is of sufficient size to carry a stock of trout.

(iii) It must be a separate stream entering the sea independently, since in a tributary of a larger stream there would be an interchange of fish between the main stream and the tributary which would make the proposed work impossible.

(iv) There must be a full stock of trout.

(v) As much of the stream as possible should be of a type of water reasonably easy to net.

(vi) There should be no dangerous pollution in any part of the stream.

(vii) The stream should be within easy driving distance of Wellington, say, 50 miles.

(viii) As much of the course as possible should be reasonably close to a road.

After a careful examination of all possible rivers within the necessary radius of Wellington the Horokiwi Stream was selected as being the most suitable.

PART II

The Environment—Inorganic

1. THE LOCALITY

The Horokiwi Stream lies on the west coast of the North Island, and enters the sea at the head of the Pahautanui inlet, about 20 miles from Wellington (see map at back). The stream, which has a total length of about 10 miles and a drainage area of 14.4 square miles, consists of two main, and approximately equal, branches which unite about 3¼ miles from the sea. The stream rises within a short distance of the sea about 2 miles south of Paekakariki, and follows a course generally slightly west of south. The combined stream (Main Water) and the western branch (Road Branch) are followed by the old main north highway, while there is a rough track up the lower part of the valley of the eastern branch (Back Branch). The headwaters lie among hills rising to between 1,000 ft. and 1,400 ft. While the valley sides are usually steep, the ridges are somewhat flattened and probably indicate an old erosion surface, belonging possibly to the Kaukau cycle (Cotton, 1912). The Back Branch follows a strikingly straight course, which lies along a major fault line. The Road Branch, on the other hand, shows a distinctly rectangular pattern, southwesterly tending sections following the line of strike alternating with southeasterly sections where the stream has cut across belts of more resistant strata. In the sections parallel to the line of strike the valley is fairly open, with some flood-plain development and usually a comparatively gentle grade. Where, however, the stream has cut through the strata a steep-sided gorge, with little or no flood-plain and a somewhat steeper grade, is generally formed.

Some of the upper tributaries of the Road Branch follow well-marked fault lines, and in the area as a whole rejuvenation of faulting has produced surface traces in the form of trenches and low scarplets. From a little above the junction of the two branches the valleys become much more open and have a wide flood-plain and, particularly in the upper portion, some low terraces. The flood-plain is interrupted not far below the junction by a short gorge section, formed by a bar of rock crossing the valley floor. In the lower part of the valley the alluvium may be of considerable depth, as a result of filling taking place following the Porirua subsidence (Adkin, 1921). In the upper part of the main valley the stream is generally close to the level of the valley floor, and some degree of aggrading appears to be taking place at many points. In the lower half of the valley, on the other hand, the stream is generally entrenched to a depth of 5 ft. to 10 ft., and seems relatively stable.

The whole drainage area lies on indurated sedimentary rocks of the Paleozoic or Mesozoic age (greywacke and argillite) which, as in all the surrounding parts

of the Wellington district, show very intense and irregular folding, the strata being in general nearly vertical.

The principal soils in the drainage area are developed, well-drained, brown silt loams, usually overlying yellow silt loams; these are found not only on the steep hilly country which surrounds the headwaters of the stream, but also on the rolling slopes which form the lower end of the tongue between the two branches, and on part of the eastern side of the lower valley. These soils occupy about 85 per cent. of the drainage area. On the lower slopes towards the seaward end of the valley well-developed, poorly-drained grey silt loams are found over yellow clay loams, these occupying about 8 per cent. of the drainage area. The floor of the main valley, and a small part of that of the Road Branch, is covered with alluvial silt loams, which are well-drained except at the lower end, where they are insufficiently elevated. These occupy about 4 per cent. of the drainage area. While the whole of the valley of the Road Branch, apart from the small alluvial pockets already mentioned, is steep and covered with brown silt loams, much of the valley of the Back Branch (about 2 per cent. of the entire drainage area) is formed of alluvial river terraces, which are generally poorly drained on account of a compact subsoil. Apart from the unleached alluviums of the main valley, the soils of the area are generally moderately leached. There has been little or no erosion of the soils of the valley walls, and the vegetative cover is only interrupted by a few small semi-stable shingle-slides in steep tributary gullies of the Road Branch. Some degree of erosion of the valley floor by the stream is however taking place in the lower part of the Road Branch and the upper part of the main valley.

Originally the entire drainage basin of the Horokiwi, like most of the Wellington district below the tree-line, was clothed in forest, or "bush," and it is clear from the accounts of early travellers through the district that this was very dense. There appear to have been no permanent Maori villages in the valley, although there were two nearby at sites close to the present townships of Pahautanui and Plimmerton. It is probable, however, that the Maoris passed through the valley when travelling or when collecting food. Settlement in the Wellington district tended to spread radially from the neighbourhood of Port Nicholson, and there was a gradual advance up the coast during the 1840s. For a time this was held up by hostile natives, and the Horokiwi valley was actually the scene of the last battle in the Wellington district. This took place in August, 1846; it ended with the defeat of the natives and finally opened the valley to undisturbed settlement. In January of the following year the construction of a road through the valley was begun. This was completed in 1849 and finally linked Wellington with the fertile Horowhenua and Manawatu plains to the north. Settlement probably followed closely on the formation of the road, but clearing of the land proceeded only slowly. Richardson (1854) who passed over the road in about 1853 states: "We reached Pahautanui where we entered the bush . . . very little land was under cultivation, though every level spot was appropriated." It is difficult to follow in any detail the process of clearing after this date, but by 1883 the New Zealand Official Handbook can record: "the Horokiwi valley, formerly dense forest, but is now cleared to a considerable extent and used for pasture": and in the same year Bishop (1882) states that "the neighbouring Pahautanui valley, although

heavily timbered in 1846, is now cleared." He also states, however, that the upper part of the road through the Horokiwi valley "overhangs a bush gully." Since this description would still apply to a small portion of this part of the road, it seems probable that the greater part of the change from the primeval state to that of the present day had already taken place by the middle 1880s, and that since that time there has been merely a small amount of additional clearing of isolated patches of bush.

At the present time the original forest has been cleared from the entire drainage basin except for a small area in the lower part of the valley of the Road Branch, and for a few small patches in tributary gullies. The rest of the area is in pasture, except for isolated lines and small plantations of trees, generally conifers. On the flood-plain of the main valley the pasture is largely used for dairy farming, but the slopes of the valley walls and the valleys of the two branches are used almost entirely for grazing sheep. Some of the steepest faces in the valley of the Road Branch had been neglected in recent years and were covered in a dense mass of gorse (*Ulex europeus*) at the time of this study. There is no definite village in the valley, but scattered farms are located at intervals throughout its length.

It was during the period when settlement and the clearing of the bush were in progress in the Horokiwi area that the acclimatization of trout in New Zealand was first undertaken. The first brown trout which are known to have been successfully reared were those imported from Tasmania by the Otago and Canterbury Acclimatization Societies in 1868 (Arthur, 1882). In 1874 trout, obtained from the South Island, were first liberated in the Wellington province, the earliest liberations being in the Waipoua, Hutt and Wainui-o-mata Rivers and the Kaiwarra Stream (Arthur, 1882, and Wairarapa Acclimatization Society, 1884). It appears to have been some years, however, before any liberations were made in the Horokiwi. In 1885, in the first report of the Wellington and Wairarapa District Acclimatization Society (later known as the Wellington Acclimatization Society) a summary of previous liberations in the Wellington province was published. In this the following paragraph appears:—

> "PORIRUA, HOROKIWI, and PAHAUTANUI. Small streams running into Porirua Harbour, suitable for trout. A few brown trout have been liberated in these streams during the past two years, say, 700 in Porirua, 500 in Pahautanui and 400 in Horokiwi. Well-grown fish are reported as having been frequently seen in all these streams, and the settlers have shown an intelligent interest in their preservation."

From this it would appear that the original liberation of brown trout in the Horokiwi consisted of about 400 fish in 1883 or 1884, and that a stock quickly became established there. These 400 fish were probably liberated as fry not long after the yolk-sac was fully absorbed, in accordance with the prevailing practice. The subsequent history of the Horokiwi stock, as to both liberations and abundance of fish, can be traced mainly from the Annual Reports of the Wellington Acclimatization Society. In 1886, the year following the extract quoted above, the corresponding paragraph reads:—

> "PORIRUA, PAHAUTANUI, and HOROKIWI. Streams into which trout have from time to time been liberated during the past three years. There are now numbers of fish in them; one weighing 8 lb. 11 oz. being lately taken there by Mr. Canavan, of Porirua."

The same report also lists the waters in which liberations had been made during the preceding year, and it does not appear that any further fish had been released in the Horokiwi. In the following year, 1887, a table of the total number of fish liberated in the various waters of the district confirms that up to that time only 400 trout had been liberated in the Horokiwi, and the comment is made that the trout are "very numerous there." In 1888 there is the statement: "Some of the streams running into Porirua Harbour are full of fish," and the Horokiwi does not appear in the list of rivers in which liberations were made. Thus, by 1888 it appears that the trout in the Horokiwi had become well established, apparently as the result of a single liberation of 400 fry in 1883 or 1884. This initial phase is fortunately quite well documented, but after 1888 no mention of the Horokiwi is made for many years, and it is not possible to ascertain the state of the trout stock there.

Except in 1910 the Annual Reports of the Wellington Acclimatization Society contain an apparently complete list of all waters in which fish had been liberated in the preceding year. No liberations in the Horokiwi are recorded until 1907, when 5,000 brown trout fry were released there; after this there is another gap until 1918 and 1919, in which years 15,000 and 7,000 brown trout fry were distributed between the Horokiwi and the nearby Little Wainui Stream; after 1919 no further liberations in the Horokiwi are recorded until 1923.

Thus, after the initial liberation, the trout in the Horokiwi were probably entirely dependent on natural reproduction until 1918, apart from the single liberation of 1907. During this period, however, liberations, generally of a few thousand fry, were recorded in the adjacent Pahautanui Stream in 1890, 1894, 1900, 1904, 1906, 1908, and 1912, while in 1892 and 1911 small liberations were made in unspecified waters by people of the same surname as residents in the Horokiwi valley. It is not impossible that some of these fish were actually released in the Horokiwi, but there is no direct evidence in support of this. Unfortunately it has not been possible to obtain any useful evidence as to the state of the trout stock during this period. Spackman, in 1892, simply records that "fly fishing can be had there," and in 1904 Hamilton states that it "contains brown and rainbow trout." Hamilton's statement is apparently based only on hearsay evidence, since he makes the same comment about nearly all the rivers in the vicinity of Wellington, none of which has contained rainbow trout in recent years. There is no record that rainbow trout were ever liberated in the Horokiwi, and the only recorded liberation of this species anywhere near was one of 4,000 fry in the Pahautanui in 1906, two years after Hamilton wrote.

In 1923 a new phase in the history of the Horokiwi began. The gradual extension of the belief that regular liberations were necessary to maintain stocks had led to a progressive increase in the extent of liberations by the Wellington Acclimatization Society. For a time this policy was not applied to the Horokiwi

and only the isolated liberations referred to above were made; but from 1923 onward the Horokiwi was regularly included among the waters in which liberations were made. The only years later than 1923 in which no liberations in the Horokiwi were recorded were 1943 and 1944 when the Society's hatchery was closed on account of the war. The total liberations by the Wellington Acclimatization Society, and the number of fish released in the Horokiwi, are shown in Table 1; the figures have been grouped in four-year periods in order to eliminate the wide fluctuations from season to season which actually took place. It will be seen that, after regular liberations had commenced there, the Horokiwi received a steadily increasing proportion of the fish released, and that this one small stream, with a drainage area comprising about 0.2 per cent. of the total area of the Wellington acclimatization district, now receives about 2 per cent. of the fish released.

TABLE 1. The numbers of trout liberated in four-year periods in the whole of the Wellington Acclimatization District and in the Horokiwi.

	Wellington District.				
Period.	Fry.	Fingerlings and Yearlings.	Total.	Horokiwi liberations.	Percentage in Horokiwi.
1883–5 ..	63,070	..	63,070	400	0·63
1886–9 ..	345,420	1,350	346,770	..	..
1890–3 ..	1,035,232	7,675	1,042,907	..	..
1894–7 ..	2,656,100	3,575	2,659,675	..	..
1898–1901 ..	1,623,300	..	1,623,300	..	..
1902–5 ..	1,582,500	..	1,582,500	..	..
1906–9 ..	1,653,000	16,500	1,669,500	5,000	0·30
1910–3 ..	1,712,000	21,100	1,733,100	..	..
1914–7 ..	2,407,250	22,000	2,429,250	..	..
1918–21 ..	3,306,000	20,150	3,326,150	11,250	0·34
1922–5 ..	3,847,600	24,900	3,872,500	12,000	0·31
1926–9 ..	5,290,500	42,000	5,332,500	55,000	1·03
1930–3 ..	6,309,000	69,400	6,378,400	80,000	1·25
1934–7 ..	5,985,000	65,500	6,050,500	78,000	1·29
1938–41 ..	5,481,000	56,000	5,537,000	60,000	1·09
1942–5 ..	1,585,000	..	1,585,000	30,000	1·89
1946–9 ..	2,861,000	31,000	2,892,000	58,700*	2·03

*Estimated; reliable figures for 1949 are not available.

This relatively high rate of stocking is probably due in part to the fact that the Horokiwi, being close to the main centres of population in the district, is generally regarded as being comparatively heavily fished. Adequate standards for testing this belief accurately are not available, but the following facts suggest that the Horokiwi does not support an unduly high proportion of the total angling in the Wellington acclimatization district. From 1939 onwards a careful check on the amount of angling in the Horokiwi has been carried out, and it has been found that in the seven seasons, between 1939 and 1942, and between 1945 and 1949, the average number of hours' angling on this stream was about 355. The seasons

1942–3, 1943–4 and 1944–5 have been ignored as the amount of angling was then greatly reduced as a result of the war. Over the same seven seasons the average revenue from fishing licences was £1,631. The great majority of the licences sold were men's whole-season licences at £1 10s., although there were also small numbers of women's, boys', and daily licences at cheaper rates. Unfortunately details of the number of each type of licence sold in the years under consideration are not available. Analysis has however been possible of the licence sales for the 1948–9 season which were at the same rates. In this season, each £1 of revenue was equivalent to 0.778 whole-season licence of some type. Applying this figure to the seasons under consideration we find the average number of whole-season licences sold was about 1,270. From 1947 to 1950 a widespread effort was made to collect diaries from as many anglers as possible throughout New Zealand. The number received was 777, and it was found that these anglers had spent an average of 88 hours fishing during the season. If this average is applied to the Wellington district, the average number of hours for the district is about 112,000. On this basis only about 0.32 per cent. of Wellington angling took place on the Horokiwi. It is probable that those anglers who keep and send in diaries are more enthusiastic and active than the average, and that they therefore spend a greater time fishing each season than the true average angler. This will reduce the total angling time to less than the above estimate, and will increase the percentage on the Horokiwi accordingly; but, even so, it is unlikely that as much as 1 per cent. of the Wellington district angling takes place there.

Some information regarding the state of the trout stock in the Horokiwi from the beginning of regular stocking in 1923 is available from the Annual Reports of the Wellington Acclimatization Society. From 1925 to 1939 a more or less stereotyped list of comments on the trout waters of the district was published. Regarding the Horokiwi, the comments in this list are:

1925: "contains brown trout."

1926–9: "contains brown trout, is improving and good sport was obtained in the (past) season."

1930–5: "contains brown trout; provided good sport during the past two seasons."

1936–9: "contains brown trout."

In addition, further comments on the Horokiwi appear elsewhere in a few of the reports; in 1933 we read that the Horokiwi "fished well, providing limit baskets" (15 fish); in 1938, "a most remarkable stream is the Horokiwi . . . to the casual observer it appears to be only a weed-infested creek, but what a stream in the earlier part of the season. It has a reputation well-known to anglers, and maintains it year after year; in fact, such streams are the salvation of many anglers when conditions are not right in our larger waters; they never let one down." In 1939 the statement appears: "limits were made at . . . Horokiwi." From the above it appears that throughout most of this period the Horokiwi contained a sufficient trout stock to provide quite good angling, although there was possibly a period of improvement in the late 1920s. Unfortunately it has not been possible to obtain any records of actual catches during this period; a small

sample of fish from which scales, now in the possession of the Fisheries Laboratory, were taken in 1926 and 1927 had an average length of 12.5 in., while another small sample taken by one angler in 1935–6 and 1936–7 seasons had an average weight of 1 lb. 3 oz. Both these figures are well within the range that might have been obtained in samples of similar size at the time of the investigation, and they do not suggest that there has been any very striking change in the size of trout in the Horokiwi during this period.

The history of the Horokiwi trout stock up to the beginning of this investigation may be summarized in three periods:

1883–1888: The period of establishment.

As a result of the initial liberation of 400 fry in 1883 or 1884, the stream at the end of this period is reported to be "full of fish."

1889–1922: The period of self-support.

Only a few isolated liberations were made, and there is no useful record of the state of the trout stock.

1923–1939: The period of liberations.

Liberations ranging between 3,000 and 30,000 fry, and averaging nearly 15,000, were made annually. During this period the stock was sufficient to yield quite good angling.

There have been various changes in the regulations controlling angling in the Horokiwi since trout were first established there. The regulations affecting this stream are partly general to the whole of New Zealand, partly local to the Wellington acclimatization district, and partly local to the Horokiwi and other specified waters. The regulations which have most effect on the activities of anglers have been those fixing:—

The open season.—Originally 1st October to 31st March. At a later date the opening day was altered to 15th September, but in 1898 it reverted to the original date of 1st October and has not since been altered. The alteration of the closing date from 31st March to the present 30th April probably took place during the 1890s.

Size limit.—The initial size limit in 1885 was 10 inches, but this was later reduced and in 1904 the size limit was 9 inches. This remained unaltered until 1932, when it was raised to 10 inches, and finally in 1939 to 11 inches.

Bag limit.—No bag limit seems to have been laid down until 1905, when it was fixed at 20 fish per day. This was not altered until 1932, when it was reduced to 15. In 1934 it was further reduced to 12, at which figure it still remains.

Permitted baits.—The regulations of 1885 allowed only "natural or artificial fly or minnow" for the whole of the Wellington district. By 1904 this had been extended to include "natural or artificial flies, insects, worms and fish." Shortly afterwards the use of natural baits was prohibited on certain waters. The list of waters was gradually extended, but it was not until 1930 that the Horokiwi was included. It was not until 1940, when this investigation had already begun, that a number of small streams in the Wellington district, including the Horokiwi, were scheduled for the use of artificial fly only.

The original regulations, drawn up in 1885, when trout were first introduced, were apparently fairly restrictive, but during the next twenty years they became somewhat easier as the trout became firmly established. Little change took place during the next thirty years, but from 1930 onwards, as the pressure of angling increased and anglers became more conscious of the need for some action to protect their fisheries, a progressive tightening of the restrictions took place.

2. THE STREAM

(a) General Description

It was originally intended to include the complete Horokiwi system in the investigation, in order to make sure that the entire trout population was under observation. It was however found impossible to cover the Back Branch in the time available except for a few casual observations, and work had to be restricted to the Main Water and the Road Branch. The discovery afterwards that the Horokiwi trout showed little movement from place to place in the stream indicated that the omission of the Back Branch would have little effect on the investigation. In the remainder of the system, the observed area extended from the mouth of the river up to the point where the Road Branch begins to break up into its main tributaries. Above this point all the streams diminish rapidly in size due to continual forking, and the few trout inhabiting these small waters are of negligible significance compared with the population of the remainder of the system. The upstream limit of the observed area is the point marked "A" on the map.

Due to the absence of significant tributaries, the stream is almost uniform in size from "A" down to the junction with the Back Branch. Here it approximately doubles its volume, and then continues to the sea with little further change. The Road Branch shows several distinct zones of strikingly different characteristics, which result from the changes already mentioned in its direction in relation to the strata. At "A" the stream is flowing in a direction generally slightly west of south, and has a relatively open valley of comparatively gentle gradient (10.8 per 1,000). There is some development of a flood-plain and the valley is floored with alluvium. The stream appears to have attained grade locally and runs between low alluvial banks, except in places where it has swung against the valley walls, producing high steep banks, either of rock or of alluvium. The bed is of alluvial gravels showing a fair degree of rounding. The valley has been cleared and the stream flows in the open through pasture land with occasional trees of various species. A short distance below "A" however the stream swings towards the south-east and has formed a narrow steep-sided gorge where it cuts through the strata. The gradient is relatively steep (17 per 1,000) and the valley walls slope steeply to the edge of the stream. There is no alluvial flood-plain and the bed is composed of large and angular stones, probably derived locally from the steep sides of the valley. This effect is to some extent natural, but it has been greatly accentuated by the addition to the river-bed of rock broken from the hillside in the construction of the road which is cut along the western wall of the gorge. In this part of the valley the land has been cleared, but has recently been neglected and is largely covered with gorse (*Ulex europeus*) which in many places almost completely encloses the stream.

Below the gorge the stream again turns south-westward and enters another comparatively open basin. Here also an alluvial flood-plain has been formed, which has reached greater development than in the upper basin; the gradient is again slight (11 per 1,000) and in the lower part there are some well-developed meanders. At some points the stream has swung against the valley wall, forming high banks of rock or alluvium, but generally the banks are low and stable. The valley is in cleared pasture and the stream flows in the open, except at a few points where it is overhung by isolated groups of trees.

Below this basin the stream swings gradually round to the south-east and closes in. In places a gorge is formed but generally there is a narrow flood-plain. The gradient is at first similar to that in the basin above but subsequently becomes rather steeper (13 per 1,000) although still less than that of the upper gorge. The degree of rounding of the stones of the stream-bed is also intermediate. The upper part of this section has been cleared but at the time of this study had been neglected for some years and was largely overgrown with gorse which overhung much of the stream. In the lower part, however, the native mixed forest remains. Here also the stream is generally overhung with trees although in a few places it runs in the open. Throughout this area the banks are usually stable, and are low, except where the stream has run up against the valley wall. In the upper part of the region the stream has become entrenched in places up to a depth of 3 ft. to 4 ft.

Below the forested area the stream emerges into an open valley and rapidly acquires a flood-plain of considerable width. There is a short section in which it is entrenched to a depth of 10 ft. to 15 ft., but below this the banks are often unstable and are low, except where the stream is cutting into old terraces forming sheer alluvial banks up to 10 ft. high. The gradient gradually decreases. At first the stream is largely overhung by trees (*Salix* sp. and *Pinus* sp.) planted along the banks, but after about 1,000 yards it emerges into the open and is only occasionally shaded by isolated groups of trees. It is in this region that the Back Branch joins the stream from the east.

About 280 yards below the junction the stream enters a short gorge section about 100 yards long where the stream has cut through the rock bar crossing the valley floor. Here there is no flood-plain, and the stream is entrenched between steep banks up to about 10 ft. in height, of either rock or alluvium. The bed however remains composed of well-rounded river gravels. This section is very largely shaded by plantations of *Pinus* sp. and *Salix* sp.

Below the gorge the stream emerges into the main valley. There is now a wide flood-plain, initially about 300 yards in width, but gradually increasing to 600 yards. The whole of the valley consists of pasture land with a few small arable patches and the stream is virtually completely open, there being a very few isolated trees distributed along its banks. In the upper part of the valley there are a number of low irregular terraces, but lower down the valley floor is virtually flat. In the main valley, two zones of approximately equal length can be distinguished. In the upper zone the stream appears to be aggrading; the banks are low except at points where the stream is cutting into an old terrace; there is a considerable development of a loose shingle flood-bed: and the course of the stream shows decided

instability at some points. Much of the stream in this area is shallow, less than 20 inches deep, but there are occasional deep pools, generally in places where the stream has run against high banks formed by old terraces.

In the lower half of the main valley the stream has either attained grade for the time being, or is still degrading, and it is generally entrenched to a depth of 6 ft. to 12 ft., the banks being usually sheer on the concave side of bends and gently sloped or terraced on the convex side. The banks are largely stable, though there are frequent small shingle beaches, and erosion of the banks is occurring at some points. There are many more pools in this zone than in the aggrading area, and their average depth is considerably greater.

The tidal region is short. At low tide the stream flows for some distance over the mud of the Pahautanui inlet, but it is very shallow and diffuse and probably of negligible importance to the trout stock. Above the level of mean high water the stream flows between definite banks; these are at first covered with salt-marsh plants, which gradually give way to gorse and grasses. The tide affects the level of the stream for a distance of about 250 yards at spring tides. Of this distance the lowest 100 yards forms a long, quiet pool and could be regarded as estuarine, but the remainder differs little from the part of the stream immediately above it.

(b) The Detailed Survey

1. Objects and Methods.

As explained above the main object of the survey was to determine the total length and area of the stream and the amount and distribution of the various types of stream and bed conditions, so that the maximum amount of information as to total populations could be deduced from the results of the sampling procedures. After consideration of various possible methods of approach, it was decided to divide the stream into a series of homogeneous sections. This method had the additional advantage that by numbering the sections it provided a rapid and accurate means of describing any point on the stream. A record book listing the dimensions and salient features of each section, and any outstanding landmarks, was prepared, and this enabled sections to be easily identified in the field on later visits. In carrying out the survey the party worked up the stream, dividing it into sections according to its appearance, and measuring and recording the following features of each section:—

(*a*) Length.
(*b*) Width.
(*c*) Depth.
(*d*) Nature of bottom.
(*e*) Current.
(*f*) Type of flow.
(*g*) Amount of cover.
(*h*) Landmarks.

(*a*) *Length.*—This was measured by laying a surveyor's chain along the stream between points selected visually as the ends of each homogeneous section. The average length of a section was 59.2 ft. in the Main Water, and 31.8 ft. in the Road Branch.

(*b*) *Width.*—This was measured from bank to bank with a surveyor's tape. The number of measurements made in each section varied according to the length and the degree of uniformity, and ranged from one to six. On the Main Water 708 measurements of width were made on the main stream, an average of 2.4 per section, at a mean spacing of 24.1 ft. On the Road Branch 1,245 measurements were made on the main stream, an average of 1.7 per section, at a mean spacing of 17.9 ft. In addition, a further 116 measurements were made on backwaters and side-channels where the stream had a divided course.

(*c*) *Depth.*—Depths were measured by means of a graduated pole, with a foot to prevent sinking into the mud. Measurements were made at the deepest point of the cross-section, and sufficient were made in each section to provide an average value for that section. In the main stream 691 measurements were made in the Main Water, and 1,340 in the Road Branch, while a further 104 were made in backwaters and side-channels.

(*d*) *Nature of Bottom.*—The bottom was examined visually and by feel, the principal categories determined being mud, sand, shingle, clay and rock. Of these shingle was by far the most abundant, and this was further subdivided according to the size of the largest stones usually present, and the degree of consolidation. In determining the size of stones a wooden disc 3.5 in. in diameter, which formed the foot of the depth pole, was used as a reference object. The presence of a silt deposit on the bed was also recorded where it occurred. Where different parts of the same section showed well-marked differences in type of bed, the relative amount of each type was recorded approximately.

(*e*) *Current.*—Currents were measured in midstream by timing a cork float over a distance of 6 ft. In order to provide an automatic measure of distance and to simplify retrieving the float, it was attached to a light thread 6 ft. in length, the time being taken until this was tightened. This method measures the surface flow, rather than either the mid-water current or the bottom current, both of which may be preferable biologically, and it may also be subject to slight errors due to the drag of the thread; it was however felt that it nevertheless provided a satisfactory basis for comparison between different sections, and had decided advantages in the simplicity of the procedure and equipment. As with width and depth measurements, sufficient readings were taken in each section to obtain an average value for the section. In all 662 measurements were made in the Main Water and 1,272 in the Road Branch, while a further 67 were made in side-channels.

(*f*) *Type of Flow.*—Four types of flow were distinguished, of which the three most frequent were *broken*, *turbulent* and *smooth*. The first was defined as having surface waves equal to at least half the depth of the water; a turbulent flow produced either small waves or distortion of vision, while a smooth flow allowed clear vision. Classification was made visually; the flow recorded for each section was that most frequent in the section, small areas of other types—e.g., a patch of turbulent water at the head of a smooth pool—being neglected. The fourth and least common type of flow recorded was *cascade*. This was the irregular flow found among large protruding stones in sections of steep gradient, and was often accompanied by some white water.

(*g*) *Amount of Cover.*—The principal types of cover recorded were:

1. Creviced or overhanging rock. This is practically restricted to gorge sections of the stream, and, where sufficiently pronounced, may provide excellent cover for fish. The length of any such rock faces, which generally occurred in pools, was determined by pacing.

2. Overhanging or fallen turfs, often with a grassy fringe. These occur where some erosion of the banks is taking place and form the most typical cover in all parts of the stream where a flood-plain is present. The cavities under and behind these turfs may be very extensive and sometimes form continuous passages of considerable length. Here also the extent of cover was estimated by pacing.

3. Cress banks. These become well developed in all quiet and open parts of the stream after continued fine weather such as prevailed at the time of the survey. Where wide, and extending into water of moderate depth, they may form useful cover for fish, but when small they are probably only of value to the invertebrate fauna. The length and width of each cress bed were estimated by pacing.

4. Accumulations of timber and brushwood. When extensive, and in deep water, these form excellent cover for both trout and eels. Such cover was however scarce in the Horokiwi except in the short stretch passing through the bush in the lower part of the Road Branch. The length and width of such accumulations were estimated by pacing. Large logs were not infrequently found partly buried in alluvium in most parts of the stream. A long overhang was frequently formed on one side of these due to the scouring action of the stream. Overhangs which formed good cover for trout were measured and recorded.

5. Protective groynes. At a number of points where the stream had threatened to undermine the road, particularly in the gorge sections of the Road Branch, protective groynes had been built of large angular stones enclosed in heavy wire-netting. The spaces between the stones were often big enough to admit quite large trout, and fish were frequently observed to shelter in them. The dimensions of such groynes, where they entered the stream, were therefore recorded.

6. Large stones. These were not common in the Horokiwi as a whole, but in a few places in the gorge section of the Road Branch there were large angular stones which provided cover for fish in the spaces beneath them. The extent of such cover was estimated visually.

7. Grass. At times of continued low water a fringe of grass often grows out into the shallower water and provides shelter for the invertebrate fauna. The length of this strip, which is usually 6 in. to 12 in. wide, was estimated by pacing.

(*h*) *Landmarks.*—The position of conspicuous landmarks which would be useful in the subsequent quick recognition of sections was recorded. Such landmarks were isolated trees, electric power poles, road defence works, culverts and tributaries.

During the period when the survey was being carried out, 15th to 23rd February and 24th March to 17th April, 1939, extremely low water conditions prevailed as a result of a long dry spell, in which only 0.90 in. of rain was recorded at the nearest rainfall station (Plimmerton) between 13th January and 17th April. As a

PLATE I. A typical reach of Zone I, showing the steep and stable banks, and the somewhat entrenched character of the stream. In this region the stickles are generally short, and deep pools are often formed against the high clay banks on the bends.

PLATE II. In Zone II M the banks are usually lower and less stable than in Zone I; stickles form a much greater proportion of the stream, and the pools are smaller and shallower.

result of these unusual conditions, which were never repeated up to the time the observations ended in October, 1941, the recorded areas of the various parts of the stream are minimum values, and are distinctly less than those normally prevailing. The areas of cover formed by fringing vegetation, i.e., grass and cress, which is dependent on stable water conditions, represent the maximum development which is likely to occur under normal conditions.

Measurements of gradient were also made by means of special surveys to determine the altitude of selected points at intervals along the stream. The results of these surveys were combined with the distances measured along the stream in the general survey for the purpose of calculating gradients.

2. Results.

(*a*) Water Types.—In order to provide a means of handling the data derived from the physical survey, and of applying the results to the estimation of populations, it was necessary to develop a scheme of classification of water types such that each section could be allocated to a particular category. For this purpose the most significant features were found to be depth and rate of flow. During the survey observations had suggested that the sections could be conveniently classified into the following types, which are already employed to a considerable extent by both fisheries workers and anglers, although generally without any attempt at precise definition:—

Pools: Water of considerable depth for the size of the stream, current generally slight, and the flow smooth apart from a small turbulent area at the head of some pools.

Flats: Water of slight to moderate current and generally smooth flow, but of less depth than in pools.

Runs: Water of moderate to rapid current and fairly deep, flow usually turbulent. In such places the stream is usually of less than average width.

Stickles: Shallow water with a rapid current and usually a broken flow. Such conditions are often described as "ripples," "rapids," or "riffles."

Cascades: Water in which a steep gradient, combined with a bed of stones or rocks large in proportion to the size of the stream, produces a very irregular rapid flow, often with some white water.

The data obtained in the survey were analysed in order to try to obtain for the Horokiwi Stream precise definitions of the above types, so that all sections could be objectively classified. As the volume of water flowing is approximately twice as great in the Main Water as in the Road Branch, the analyses were carried out separately for these two regions. It is apparent from the above descriptions that depth, velocity and type of flow generally determine the type to which a section belongs. Of these the two former are susceptible to precise measurement and were used as a basis for the analysis, while the type of flow provides a useful check on the results. General observations suggested that the relation between depth and width might form a better basis for classification than absolute depth, and might have the additional advantage of being more independent of volume of flow.

Analyses were therefore based both on the depth-width ratio and on the absolute depth. It was found rather unexpectedly that absolute depth gave decidedly more satisfactory results, and it was therefore used in classifying the sections.

TABLE 2. The distribution of mean depth and current in Main Water sections.

Current in ft./sec.	Depth in Feet. 0 to 0·24	0·25 to 0·49	0·50 to 0·74	0·75 to 0·99	1·00 to 1·24	1·25 to 1·49	1·50 to 1·74	1·75 to 1·99	2·00 to 2·24	2·25 to 2·49	2·50 to 2·74	2·75 to 2·99	3·00 to 3·24	3·25 to 3·49	3·50 to 3·74	3·75 to 3·99	4·00 to 4·24
3·75–3·99 ..	..	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..
3·50–3·74 ..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
3·25–3·49 ..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
3·00–3·24 ..	1	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
2·75–2·99 ..	..	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
2·50–2·74 ..	..	5	5	1	..	..	..	..	..	..	..	..	..	..	..	..	..
2·25–2·49 ..	2	17	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..
2·00–2·24 ..	1	24	11	2	1	..	..	..	..	..	..	..	..	..	..	..	..
1·75–1·99 ..	..	13	4	2	1	1	..	..	..	..	..	..	..	..	..	..	..
1·50–1·74 ..	1	14	11	4	2	1	..	..	2	..	..	..	..	..	..	..	..
1·25–1·49 ..	..	6	7	1	3	2	..	1	..	..	..	..	..	..	..	..	..
1·00–1·24 ..	..	4	9	9	6	4	..	..	..	..	..	..	..	..	..	..	..
0·75–0·99 ..	..	..	12	12	8	4	2	3	3	..	2	..	..	..	..	..	..
0·50–0·74 ..	..	..	3	2	5	5	1	3	5	4	..	4	..	..	..	..	..
0·25–0·49 ..	..	..	..	1	..	..	4	4	2	3	..	1	1	..	..	..	..
0 –0·24 ..	..	..	..	..	..	1	..	..	..	..	..	3	1	..	..	..	1

For each section the mean current and depth were determined from the various field observations. Table 2 shows the number of occurrences of each combination of current and depth in the Main Water; the mean values are assembled in groups of 0.25 ft. per sec. and 0.25 ft. respectively. Inspection of the results shows that the sections fall most abundantly into the following groups:—

Current		Depth
(1) 1.50 to 2.49 ft. per sec.	....	0.25 to 0.74 ft.
(2) 0.75 to 1.24 ft. per sec.	....	0.50 to 1.24 ft.
(3) 0.25 to 0.99 ft. per sec.	....	1.75 to 2.24 ft.
(4) 0 to 0.74 ft. per sec.	....	2.75 to 3.24 ft.

Using these groups as nuclei the sections were divided up as shown by the lines in the table, and it was then found that there was also a distinct group of sections having currents greater than 1.24 ft. per sec. and depths greater than 0.74 ft., although no separate nucleus appears in this part of the table. The distribution of flow types within these five groups of sections was examined with the results shown in Table 3. It is apparent that each group of sections is characterized by a particular

TABLE 3. Distribution of flow-types in relation to depth-current groups for Main Water sections.

Current (ft./sec.).	Depth (ft.).	Broken No.	Broken %	Turbulent. No.	Turbulent. %	Smooth. No.	Smooth. %
Over 1·24	Under 0·75 ..	107	*80*	22	*17*	4	*3*
Over 1·24	Over 0·74 ..	2	*8*	18	*75*	4	*17*
Under 1·25	Under 1·50 ..	1	*1*	19	*22*	65	*77*
Under 1·25	1·50–2·24 ..	0	*0*	2	*6*	32	*94*
Under 1·25	Over 2·24 ..	0	*0*	0	*0*	13	*100*

flow type. Cascades do not occur in the Main Water on account of the scarcity of large stones. When the characteristics of the various groups of sections are compared with the general descriptions of water types given above, they appear to provide a satisfactory and precise means of classifying the sections into water types. This has been done using the following definitions:—

Stickle	Current	Over 1.24 ft. per sec.
	Depth	Under 0.75 ft.
Run	Current	Over 1.24 ft. per sec.
	Depth	Over 0.74 ft.
Flat	Current	Under 1.25 ft. per sec.
	Depth	Under 1.50 ft.

Pools were subdivided into two groups—

Pools	Current	Under 1.25 ft. per sec.
	Depth	1.50 to 2.24 ft.
Deep pools	Current	Under 1.25 ft. per sec.
	Depth	Over 2.24 ft.

Classified in this way, the 289 sections of the Main Water were found to consist of 133 stickles, 24 runs, 85 flats, 34 pools and 13 deep pools.

TABLE 4. The distribution of mean depth and current in Road Branch sections.

Current in ft./sec.	Depth in Feet. 0 to 0·24.	0·25 to 0·49.	0·50 to 0·74.	0·75 to 0·99.	1·00 to 1·24.	1·25 to 1·49.	1·50 to 1·74.	1·75 to 1·99.	2·00 to 2·24.	2·25 to 2·49.	2·50 to 2·74.	2·75 to 2·99.
3·00–3·24 ..	1	2	..	..	..	..	..	..	..	..	..	..
2·75–2·99 ..	..	1	..	..	..	..	..	..	..	..	..	..
2·50–2·74 ..	..	4	..	..	..	..	..	..	..	..	..	..
2·25–2·49 ..	3	16	..	..	..	..	..	..	..	..	..	..
2·00–2·24 ..	11	39	2	1	..	..	..	..	..	..	..	..
1·75–1·99 ..	7	24	2	..	..	..	..	..	..	..	..	..
1·50–1·74 ..	20	84	13	1	1	..	..	..	..	..	..	..
1·25–1·49 ..	9	61	22	4	..	..	..	..	..	..	..	..
1·00–1·24 ..	5	54	28	12	1	..	..	..	..	..	..	..
0·75–0·99 ..	1	14	44	12	7	3	2	..	..	..	..	..
0·50–0·74 ..	..	11	39	23	16	6	4	..	..	..	1	..
0·25–0·49 ..	..	..	6	17	19	14	10	3	4	1	3	1
0 –0·24 ..	..	..	..	..	1	4	2	2	1	1	..	..

TABLE 5. Distribution of flow-types in relation to depth-current groups for Road Branch sections.

Current (ft./sec.)	Depth (ft.).	Cascade. No.	%	Broken. No.	%	Turbulent. No.	%	Smooth. No.	%
Over 0·99	Under 0·50 ..	49	*14*	226	*66*	66	*20*	0	*0*
Over 0·99	Over 0·49 ..	4	*4*	13	*15*	59	*68*	11	*13*
Under 1·00	Under 1·25 ..	1	*1*	2	*1*	55	*26*	152	*72*
Under 1·00	1·25–2·24 ..	0	*0*	0	*0*	0	*0*	55	*100*
Under 1·00	Over 2·24 ..	0	*0*	0	*0*	0	*0*	7	*100*

The same system of analysis was applied to the results of the survey of the Road Branch, the results being given in Tables 4 and 5. Although the nuclei are not as apparent as in the Main Water, the distribution is of the same general type, and a similar scheme of classification has therefore been fitted to it, and is indicated by lines in the table. The definitions of water types in the Road Branch are therefore:—

Cascade and Stickle	Current	Over 0.99 ft. per sec.
	Depth	Over 0.50 ft.

(*Cascade* and *Stickle* are distinguished according to the flow type recorded in the field.)

Run	Current	Over 0.99 ft. per sec.
	Depth	Over 0.49 ft.
Flat	Current	Under 1.0 ft. per sec.
	Depth	Under 1.25 ft.
Pool	Current	Under 1.0 ft. per sec.
	Depth	1.25 to 2.24 ft.
Deep pool	Current	Under 1.0 ft. per sec.
	Depth	Over 2.24 ft.

On this basis the 702 sections of the Road Branch consisted of 49 cascades, 291 stickles, 88 runs, 210 flats, 55 pools and 7 deep pools, and 2 dry sections.

On account of differences in the nature of the trout population, it was found desirable to divide the stream into five zones. The second of these zones included

TABLE 6. Dimensions and features of the zones into which the Horokiwi was divided.

ZONE	SECTION NUMBERS	LENGTH (ft.).	AREA (sq. ft.). Main Stream	Backwaters and Collaterals.	Total.	DESCRIPTION
I ..	M1–195	10,391	148,327	7,032	155,359	Stream stable, slightly entrenched, in wide, grassy, alluvial valley.
II M ..	M196–289	6,678	89,526	1,549	91,075	Stream aggrading, rather unstable, in wide grassy, alluvial valley.
II R ..	R1–187	6,294	60,858	599	61,457	Stream aggrading, rather unstable, in wide, grassy, alluvial valley.
III ..	R188–447	8,922	84,680	2,432	87,112	Stream stable, slightly entrenched, in steep-sided valley with narrow, alluvial floor. Valley largely bush-covered.
IV ..	R448–637	5,255	40,462	1,244	41,706	Stream stable, not entrenched, in narrow, steep-sided gorge, largely covered in gorse.
V ..	R638–702	1,728	12,863	195	13,058	Stream stable, not entrenched, in open grassy, alluvial basin between steep hills.

the upper part of the Main Water and the lowest part of the Road Branch, and was consequently divided into two sub-zones, being separated at the junction of the Main Water and Road Branch. The location, length and brief description of these zones are given in Table 6. As these zones appeared to show in many respects distinct but homogeneous conditions, they have been used as a basis for

Table 7. The number of sections, total area in sq. ft., and percentage area composed of each water type in each zone.

Zone.	Cascade.			Stickle			Run.			Flat.			Pool.			Deep Pool		
	No.	Area.	% Area.	No.	Area.	% Area.	No.	Area.	% Area.	No.	Area.	% Area.	No.	Area.	% Area.	No.	Area.	% Area.
I	0	0	..	86	56,281	*36·3*	14	5,902	*3·8*	57	46,733	*30·0*	25	34,041	*21·9*	13	12,402	*8·0*
II M ..	0	0	..	47	54,686	*60·1*	10	2,769	*3·0*	28	21,278	*23·3*	9	12,341	*13·4*	0	0	..
II R ..	3	3,376	*5·5*	85	28,945	*47·3*	37	7,576	*12·3*	54	19,654	*32·1*	7	1,388	*2·3*	1	518	*0·8*
III	24	14,537	*16·7*	94	21,958	*25·3*	20	3,158	*3·6*	92	33,343	*38·4*	26	12,387	*14·3*	4	1,487	*1·7*
IV	22	8,687	*20·8*	75	11,598	*27·8*	22	2,233	*5·4*	50	12,690	*30·4*	17	5,905	*14·2*	2	593	*1·4*
V	0	0	..	38	5,986	*45·7*	7	679	*5·2*	15	4,810	*36·8*	5	1,583	*12·3*	0	0	..

Table 8. The average dimensions (in ft.) in sections of each water type in each zone.

Zone.	Cascade.			Stickle			Run.			Flat			Pool.			Deep Pool.		
	Mean Length.	Mean Width.	Mean Area.	Mean Length.	Mean Width.	Mean Area.	Mean Length.	Mean Width.	Mean Area.	Mean Length.	Mean Width.	Mean Area.	Mean Length.	Mean Width.	Mean Area.	Mean Length.	Mean Width.	Mean Area.
I	..	..	..	49·6	12·9	641	38·5	10·8	416	50·2	14·3	716	80·3	16·9	1,361	55·0	17·3	954
II M ..	..	..	..	91·7	12·7	1,161	26·5	10·4	277	49·0	14·4	708	81·1	16·9	1,371	..	..	..
II R ..	101·8	11·0	1,125	34·4	9·8	337	25·7	8·0	205	35·0	10·2	359	26·7	7·4	196	31·0	16·7	518
III	67·4	8·9	599	25·8	9·0	232	25·6	6·1	158	36·2	9·4	340	41·5	11·5	476	34·0	10·9	372
IV	49·9	7·9	395	20·6	7·1	146	18·1	5·6	102	30·2	8·0	242	37·2	9·3	347	35·5	8·3	296
V	..	..	..	22·2	7·0	156	17·8	5·4	97	38·7	8·0	311	35·5	8·9	317	..	..	..

all the quantitative studies of this stream, each zone being treated as a separate unit. The extent of the occurrence of the different water types in each zone is shown in Table 7, and some definite differences between the zones are apparent. The most striking of these is that between Zones I and II M, the two parts of the Main Water. In Zone I, stickles, flats, and the two types of pool each occupy about one-third of the area of the stream; but in Zone II M, the stickles occupy 60 per cent. of the stream bed, and the flats, and, even more, the pools are greatly reduced in total extent. This difference seems to be closely correlated with the fact that in Zone II M the stream bed is unstable and apparently aggrading, so that the deeper water of the flats and pools is perpetually tending to be filled up by the moving shingle. In Zone I on the other hand more stable conditions prevail and consequently deep and permanent pools are formed. The contrast is actually even greater than would appear from the figures since four out of the nine pools in Zone II M occur in or close to the short stretch of gorge-like water near the head of the zone, where the rocky banks produce a local stability. Since the survey was carried out at the beginning of the observations, the data in the foregoing tables, as well as that used in determining the boundaries of the zones, all refer to conditions at that time. In 1941, as a result of a succession of severe floods, the lower end of the aggrading region moved several hundred yards downstream from the boundary between Zones I and II M. As a consequence, conditions in this part of Zone I changed from those typical of this zone to those typical of Zone II M.

A similar contrast is shown in the Road Branch zones; Zone II R resembles Zone II M in being actively aggrading and has a much smaller proportion of pools than the more stable zones further upstream. The other three zones show relatively slight differences in the occurrence of the different water types. Zones III and IV are characterized by the occurrence of frequent cascades, due to the relative abundance of large stones which are absent further upstream. A further noticeable difference between the zones is the relatively greater extent of the rapid water types—cascades and stickles—in Zone IV compared to Zones III and V, and the correspondingly small quantity of flats. This is probably the result of the somewhat steeper gradient which exists in Zone IV. The variations in the extent of the different water types are shown diagrammatically in Fig. 1. This emphasises the relative uniformity of conditions in the upper, confined portions of the Road Branch as compared with the great variations which differences in the extent of erosive activity bring about in the open valleys of the lower part of the Road Branch and of the Main Water.

Table 8 shows the average dimensions of each type of section in each zone. It is noticeable that in general the average dimensions of sections of a given water type, and particularly the widths, are very similar in adjacent zones wherever the volume of water flowing is about the same. This resemblance is especially striking between Zones I and II M, and between Zones IV and V. In the lower zones of the Road Branch, however, the increase in size of the stream, due to a number of small inflows, is sufficient to cause a general and progressive increase in width downstream. With very few exceptions the relations between the dimensions of the various types of sections are the same in all zones, regardless of the volume of

flow. In almost every case the four main types in descending order of width are pool, flat, stickle, run; deep pools generally resemble other pools in width, while cascades are usually similar to stickles. In general a similar relationship holds as

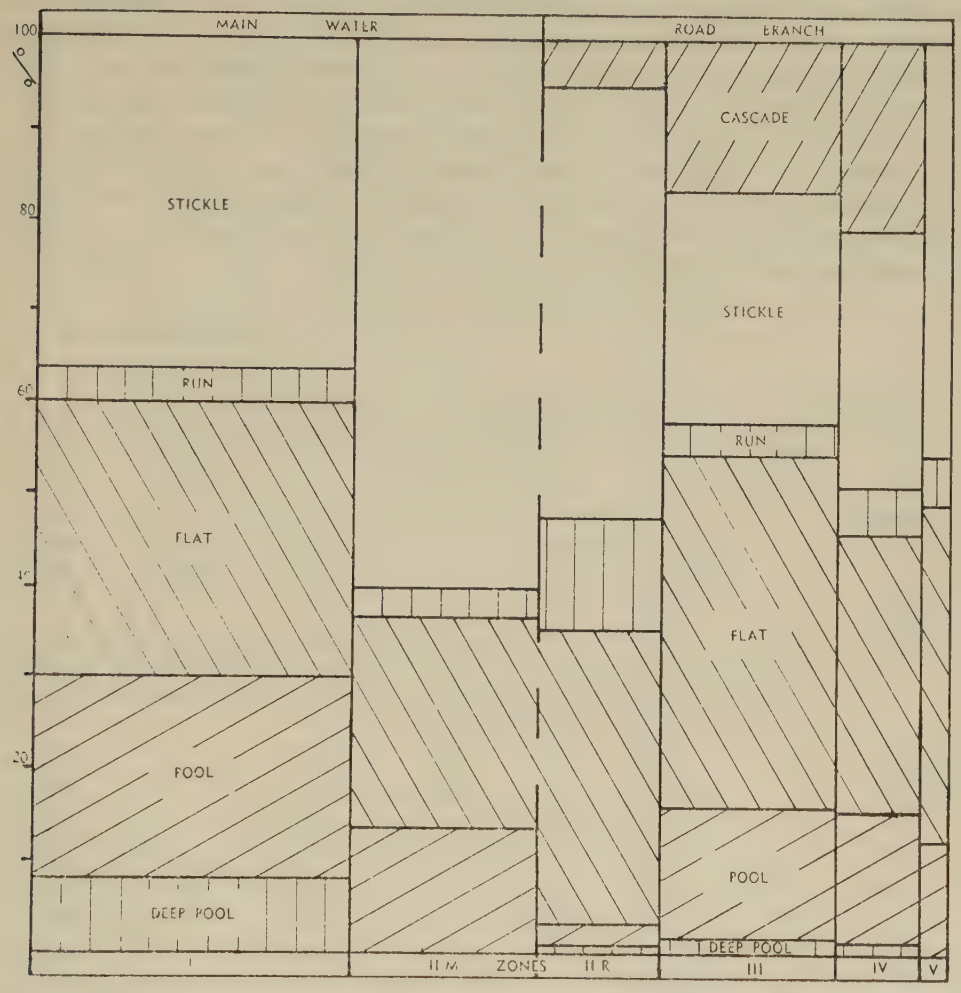

FIGURE 1. The percentage of each water type in each zone: the widths of the columns are proportional to the total areas of the zones.

regards the length of sections although there is rather more variation in this respect from zone to zone. Cascades where they occur are, however, consistently longer than any other type of section. The most noticeable exception to these general tendencies is found in the aggrading lowest part of the Road Branch, Zone II R. Here such pools as occur are not only few in number but also small in size; in this zone they have the smallest area of any type of section, although in almost all other zones they have the largest.

As the areas of the sections and zones are to be used in connection with the quantitative studies of the trout and the bottom fauna populations, it is desirable to give consideration to the degree of accuracy with which they have been determined. Area has been measured as the product of length and width; of these

length is the more accurate, since it is the measurement of a single dimension—the distance along the centre line of the stream—and as such is subject only to minor errors of reading or of laying the chain. Width, on the other hand, is subject in addition to the possibility of substantial sampling errors, since the width of the stream is varying irregularly all the time, and the measurements form only a set of samples from an infinite possible series. The sample widths are not a truly random selection, since the procedure followed was to take a representative selection in each section, and there was therefore a tendency to take more measurements in a section with variable widths than in one of similar length which was uniform. The readings will however give an indication of the degree of variation which occurs in the width of the stream, and will probably tend to give a rather high value for the degree of scatter of the readings.

TABLE 9. The percentage of each type of substratum in each water type in each zone.

WATER TYPE	ZONE.	SUBSTRATUM. Silt and Mud.	Sand.	Clay.	Rock and Concrete.	Shingle.
Cascade	II R	..	..	..	..	100·0
	III	..	..	0·2	..	99·8
	IV	..	..	..	0·5	99·5
Stickle	I	..	..	0·3	..	99·7
	II M	..	..	0·4	..	99·6
	II R	..	..	..	..	100·0
	III	..	..	..	0·1(wood)	99·9
	IV	..	..	0·5	1·2	98·3
	V	..	..	..	..	100·0
Run	I	..	..	1·6	..	98·4
	II M	..	..	..	..	100·0
	II R	1·2	..	..	..	98·8
	III	..	..	..	13·2	86·8
	IV	1·9	..	1·7	2·9	93·5
	V	..	..	..	..	100·0
Flat	I	..	..	1·7	..	98·3
	II M	..	..	..	0·3	99·7
	II R	3·8	..	0·4	0·9	94·9
	III	4·3	..	0·2	0·3	95·2
	IV	5·7	..	0·5	1·1	92·7
	V	8·9	..	..	..	91·1
Pool	I	5·6	9·5	4·2	..	80·7
	II M	..	..	..	3·5	96·5
	II R	..	6·6	..	..	93·4
	III	2·7	..	0·4	3·8	93·1
	IV	2·0	..	..	4·6	93·4
	V	..	..	..	13·0	87·0
Deep Pool	I	19·3	..	3·2	..	77·5
	II R	..	..	..	..	100·0
	III	10·2	..	..	..	89·8
	IV	..	..	..	..	100·0

The standard and relative deviations and the 95 per cent. confidence limits of the means were therefore calculated for each type of section in each zone for which 50 or more readings were available. The standard deviation ranged between 2.4 and 4.6 ft., while the relative deviation ranged from 0.22 to 0.43 with a mean of 0.35. The 95 per cent. confidence limits ranged from ± 0.033 to ± 0.092 of the mean with an average value of ± 0.059. Although the relative range of the 95 per cent. confidence limit would be greater for groups in which fewer readings were taken, the effect on the reliability of the estimates of the total area of the zones would not be correspondingly increased, because of the relatively small proportion of the zonal areas formed by these groups. It appears therefore that the areas of the zones at the time of the survey can be taken as being correct to within ± 5 per cent. with 95 per cent. confidence. This margin of error is probably small compared with the changes in total stream area which occur as the water level rises or falls.

(*b*) Bed Types.—The predominant type of stream bed in the Horokiwi was found to be a graded mixture of silt, sand, and small stones of various sizes such as is usually described as "gravel," or, in New Zealand, as "shingle." This type of bed was by far the most abundant in all parts of the stream and in all types of water. In the Main Water it formed 94.5 per cent. of the total bed of the main stream, and in another 0.5 per cent. the nature of the bed was not recorded, but was very probably also shingle. In the Road Branch, 96.5 per cent. of the main

Table 10. The percentage distribution of maximum size of shingle in sections of each water type in each zone; also the mean maximum size of shingle in each zone.

Zone	Water Type	Maximum Size of Shingle in Inches											Mean Max. Size
		0–1	2–3	4–5	6–7	8–9	10–11	12–13	14–15	16–17	18–19	Over 19	
I	Stickle ..	2·2	38·3	23·0	16·5	12·1	7·5	..	..	..	..	..	
	Run ..	13·3	53·3	16·6	8·4	6·8	..	..	..	..	..	..	
	Flat ..	4·2	47·8	17·4	20·8	4·7	0·4	..	..	..	..	..	
	Pool ..	33·4	14·5	27·8	4·2	0·7	..	..	..	..	..	..	
	Deep Pool ..	43·3	28·5	..	5·6	..	..	..	..	..	..	..	3·89
II M	Stickle ..	0·4	20·2	43·1	12·6	14·6	4·5	4·2	..	..	..	..	
	Run ..	..	27·0	24·6	29·0	8·9	10·6	..	..	..	..	..	
	Flat ..	4·0	34·3	37·7	11·3	5·1	5·3	2·1	..	..	..	..	
	Pool ..	..	47·7	39·0	2·7	7·0	..	..	..	..	..	..	5·15
II R	Cascade ..	..	..	..	..	20·6	29·3	..	20·6	..	..	29·3	
	Stickle ..	..	0·2	7·4	13·1	41·2	20·8	4·3	7·9	0·7	0·9	3·6	
	Run ..	..	0·5	5·0	19·4	37·1	18·6	8·5	5·0	0·9	1·8	2·0	
	Flat ..	..	1·8	11·1	14·1	42·0	7·0	4·6	8·3	0·7	4·3	1·1	
	Pool ..	..	..	27·2	25·9	17·3	8·9	14·3	..	..	..	..	
	Deep Pool ..	..	37·5	..	37·5	12·5	..	..	12·5	..	..	..	9·85
III	Cascade ..	..	2·2	1·1	14·1	28·7	5·2	9·0	9·5	..	20·9	9·1	
	Stickle ..	..	2·9	15·7	29·5	17·5	9·5	8·2	7·0	1·2	6·6	1·9	
	Run ..	..	2·7	11·6	19·0	11·1	8·4	7·3	..	..	11·7	15·0	
	Flat ..	..	5·3	29·4	13·1	21·2	7·3	6·5	3·4	..	5·2	3·1	
	Pool ..	3·0	6·7	14·3	38·5	8·5	8·0	2·9	5·2	..	2·4	3·5	
	Deep Pool ..	..	..	36·2	43·4	..	10·2	..	..	..	..	..	9·51
IV	Cascade ..	..	1·9	16·5	20·3	11·4	3·6	5·4	14·2	..	16·8	6·1	
	Stickle ..	0·9	3·5	20·8	11·4	29·8	6·9	12·5	6·0	..	4·9	1·4	
	Run ..	..	..	12·2	17·5	21·6	9·4	8·7	4·2	..	12·8	7·2	
	Flat ..	..	1·6	17·9	19·4	18·7	5·1	5·8	12·4	..	10·2	1·6	
	Pool ..	..	10·5	19·0	15·5	27·5	3·3	8·0	..	7·1	0·6	1·9	
	Deep Pool ..	..	38·8	12·8	48·4	..	..	..	..	..	..	..	9·73
V	Stickle ..	..	21·0	30·1	28·0	17·7	0·6	1·6	..	..	1·0	..	
	Run ..	..	46·3	15·3	11·9	26·4	..	..	..	..	..	..	
	Flat ..	0·8	8·9	31·2	28·8	7·5	9·9	4·0	..	..	..	..	
	Pool ..	12·3	18·7	10·1	30·2	3·2	..	12·3	..	..	..	..	5·80

stream area was composed of shingle, and the nature of another 0.25 per cent. was unrecorded and was possibly shingle. More detailed distribution of the various types of substratum is shown in Table 9. It is evident that, while shingle is the predominant substratum in all cases, its proportion of the total stream bed increases progressively as the characteristic current increases. This is partly because the relatively fine silts and sands are easily disturbed and are therefore largely restricted to the quiet water conditions found in deep pools, pools and flats. In addition the firmer strata, underlying the alluvium, which consist generally of clays in the Main Water and of rock in the Road Branch, also tend to be exposed as a part of the stream bed at the points of maximum erosion. This occurs on bends where lateral corrasion is in progress with the consequent formation of pools, and also in areas where the combination of relatively rapid current and considerable depth of water tends to scour the stream bed and to form runs. A small amount of concrete is included among the rock of Zone II R; this is found at a point where the stream flows over the concrete foundations of a bridge.

TABLE 11. The percentage of the shingle bed coated with silt in each water type in each zone.

ZONE.	WATER TYPE				
	Cascade.	Stickle.	Run.	Flat.	Pool.	Deep Pool.
I		1·4	0	33·9	48·8	68·3
II M		0	24·4	23·9	69·0	..
II R	0	0	0	19·7	51·1	24·7
III	0	0	2·6	50·3	85·7	100·0
IV	0	0	7·1	42·0	93·5	100·0
V		0	0	16·3	36·0	..
Combined	0	0·4	4·1	34·3	64·0	71·3

Considerable variations were also found in different parts of the river in the size of stones in the shingle. Table 10 shows for each water type in each zone the percentage of the bed of the main stream in which the normal maximum size of the shingle fell in each 2 in. group. It appears that, although the average maximum size in each zone tends to increase with increasing characteristic current, these differences are generally small compared with those which occur between the different zones. The differences between the zones are clearly shown by the average maximum sizes in each zone, and it is apparent that, in this respect, the stream may be divided into three regions. In the Main Water the stones are relatively small, but there is an increase in size upstream from Zone I to Zone II M; in Zones II R, III and IV in the Road Branch comparatively large stones are widely distributed; these probably have their origin in the gorge reaches, particularly of Zone IV; in the upper part of the Road Branch in Zone V an alluvial flood-plain of relatively fine material occurs. The table also shows that in Zones II R, III and IV there is a very much greater range of sizes than in the other parts of the stream.

A silt coating over the stones of a shingle bed, like a silt bed, was found only

under fairly quiet conditions. The occurrences of such a coating were recorded during the survey and the results are shown in Table 11. It appears that such a coating is a usual feature of deep pools and pools, and is found over about one-third the area of flats, but that it is rarely or never found in the sections with a more rapid characteristic flow. Since the survey was carried out during a period of exceptionally low water in late summer, these results probably represent the maximum occurrence of a silt coating on the shingle bed and such a coating would usually be much less extensive, particularly during the winter.

The degree of looseness or consolidation allocated to the shingle bed in each section was based on purely subjective impressions, five categories being distinguished. Analysis of the results shows that the great bulk of the sections fall into the central categories corresponding to a moderate degree of consolidation, and that there is little significant variation between different classes of sections. There appears to be a slight tendency for the bed to become progressively looser upstream, and for flats, stickles and cascades to have firmer beds than pools or runs, but the results seem to be of little practical significance.

(*c*) Cover.—For purposes of analysis the covers were grouped in two main categories:

Temporary cover, comprising only grass and cress banks. These are essentially seasonal in development, and in addition are easily destroyed by quite small floods. They provide poor cover for all but small fish, except for extensive cress banks growing into deep water.

Permanent cover, comprising all other types. Although all of these are liable to gradual change in course of time, or to violent change in heavy floods, they are far more permanent than the banks of vegetation. Most types usually provide effective shelter for fish of all sizes.

Table 12 shows the amount of each type of cover in each water type in each zone. This has been expressed as a percentage of the total length of bank, i.e.,

Table 12. The percentage of the total bank length occupied by temporary and permanent cover in each water type in each zone.

Zone.	Water Types.															
	Cascade.		Stickle.		Run.		Flat.		Pool.		Deep Pool.		Combined.	
	Temp.	Perm.	Temp.	Perm.	Temp.	Perm.	Temp.	Perm.	Temp.	Perm.	Temp.	Perm.	Temp.	Perm.
I	..	..	..	..	28·8	11·9	18·5	23·2	30·3	18·1	21·5	30·7	15·2	44·6	26·9	20·0
II M	..	..	..	..	40·4	12·5	23·2	29·8	40·6	17·8	39·2	33·4	..	..	39·7	16·6
II R	..	..	34·1	13·3	40·7	12·6	34·7	18·4	30·2	24·7	25·9	41·7	0	64·5	35·3	18·1
III	..	..	29·0	15·1	27·4	16·6	9·8	13·3	32·7	26·8	20·7	38·4	33·2	42·8	28·1	23·1
IV	..	..	14·9	15·3	13·1	9·9	7·0	17·0	16·1	17·8	15·2	31·1	1·4	42·2	14·0	16·7
V	..	..	..	..	47·2	9·1	53·6	8·4	41·8	9·3	29·6	29·0	..	..	44·0	11·1
Combined	..	..	24·2	14·9	33·0	12·5	22·8	18·8	31·0	20·9	24·1	33·8	16·2	45·0	29·7	19·0

twice the stream length, which is occupied by each type. Certain definite trends are evident. Permanent cover is clearly associated with depth of water and quiet flow, being much more abundant in pools (including deep pools) and in flats than in shallower and more rapid water. Temporary cover, which is generally formed where shallow stream margins permit the invasion of the stream by vegetation,

is correspondingly associated with shallow water, being most abundant in flats and stickles, and least abundant in deep pools. The well-marked differences in the amount of cover in the different zones arise largely from the same causes. Comparison of the percentage of temporary cover in the different zones with the proportion of the zone which is composed of flats and stickles shows almost linear relation between the two. Despite this, it is however probable that the pronounced scarcity of temporary cover in Zone IV is due not only to this effect but also to the great extent to which the stream is shaded in this zone by the steep gorge-like valley walls and the numerous overhanging gorse bushes. The correlation with the occurrence of the various water types is not so pronounced in the case of permanent cover, but it is noticeable that Zones I and III, with relatively abundant pools and flats, possess more permanent cover than do Zones II M, II R and V which are comparatively poor in these water types. An apparent anomaly is presented by the scarcity of permanent cover in Zone IV, but this is due to the fact that the gorge-like nature of the valley and the absence of an alluvial flood-plain in this region prevent the frequent formation of overhanging banks which are the most abundant form of permanent cover in the other zones.

(*d*) Gradient.—The results of the measurement of gradient are shown in Fig. 2 and Table 13. It is apparent that in general the Horokiwi conforms to the most usual pattern in having a gradient which decreases as the stream

Table 13. Height above sea level, fall, length and gradient for each zone. (The points used in determining heights were sometimes slightly away from the zone boundaries; thus the lengths used here may differ slightly from the true lengths of the zones.)

Zone.	Height at Foot (ft.).	Height at Top (ft.).	Fall (ft.).	Length (ft.).	Gradient	
					Per 1,000.	Ft./mile.
I	0	57·1	57·1	10,367	5·48	28·9
II M	57·1	115·1	58·0	6,703	8·66	45·7
II R	115·1	194·2	79·1	6,218	12·75	67·4
III	194·2	304·0	109·8	8,888	12·34	65·2
IV	304·0	396·6	92·6	5,433	17·07	90·2
V	396·6	414·6	18·0	1,660	10·85	57·4

descends. Certain exceptions occur due to the relation between the course of the stream and the geological structures over which it flows. At three points the gradient is reduced above a rock barrier, and then increases abruptly as the stream breaks through. These barriers with increased gradients occur in Zone IV, at the lower end of Zone III, and in Zone II M a short distance below the junction.

The gradient ranges between 5 per 1,000 in the lowest part of the course and about 17 per 1,000 in Zone IV. Since throughout its length the stream is manifestly a suitable habitat for brown trout, it is of interest to compare the above figures with those recorded as suitable for trout by other workers. Huet (1946) has discussed the relation between the gradient and the composition of the fish

population in the rivers of the Belgian Ardennes. He has concluded that waters with a gradient greater than 3 per 1,000, and even as great as 37.5 per 1,000, are almost exclusively occupied by trout, although some grayling and chub occur in gradients up to 6.5 per 1,000. Trout are also the dominant components of a mixed fish fauna in gradients as low as 1.5 per 1,000 and occur in small numbers down to 0.75 per 1,000, but not in lower gradients than this. The gradients found in the Horokiwi are therefore very similar to those occurring in the waters occupied almost exclusively by trout in Belgium.

On the other hand, Hobbs (1948), when discussing the major trout rivers of the east coast of the South Island of New Zealand, has pointed out that the most productive parts of these have gradients not exceeding 17 ft. per mile (3.2 per 1,000). Thus, the most productive parts of these rivers have gradients which lie below the range which has been found to be typical of trout waters in Belgium, and below the range found in the Horokiwi. Hobbs has however pointed out that much steeper gradients occur in other New Zealand waters where the stability of the bed is increased by the presence of boulders and rocks, and that the limits he indicates apply only to streams with gravel beds flowing over readily erodible plains. It appears however that the range of gradients which will be suitable for trout in a given river system is determined not only by the nature of the bed but also by the volume of flow. Huet, in stating his "règle des pentes" as follows, has recognized the necessity of taking the size of the stream into account:

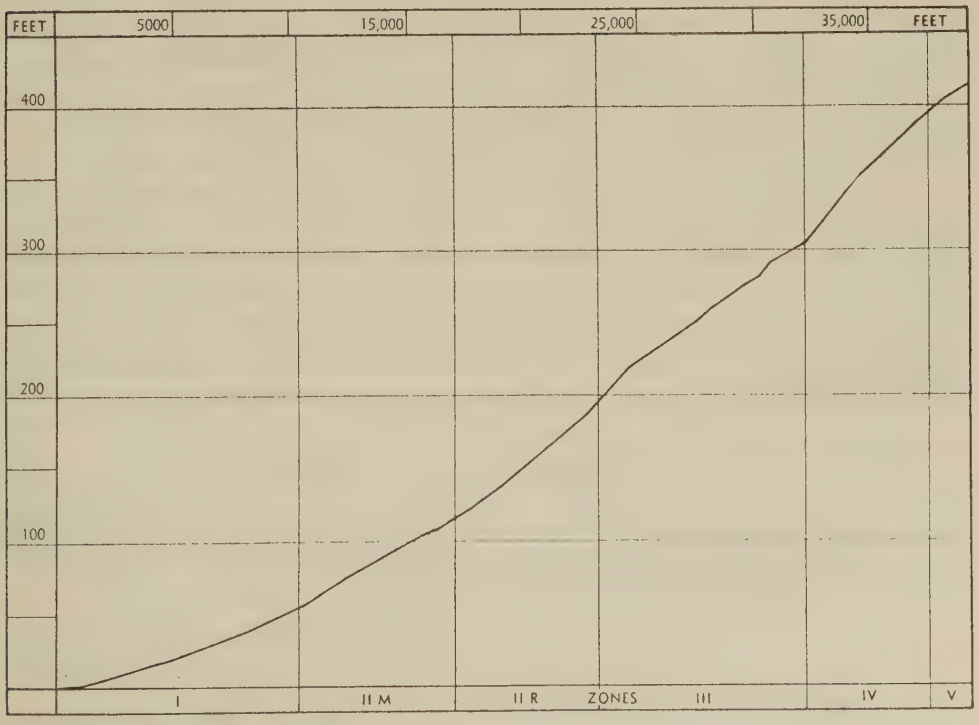

FIGURE 2. The profile of the Main Water and Road Branch: the height above sea-level plotted against the distance from the mouth of the stream.

"Dans une région biogéographique déterminée, des eaux courantes de même importance quant à la largeur et la profondeur, et possédant des pentes comparables, ont des caractères biologiques, et spécialement des populations piscicoles, analogues."

Gradient in itself does not seem likely to have any effect upon the fish population of a stream, but its action will be exerted through its influence on such biologically important factors as the stability of the bed, the presence of suitable gravel for successful spawning, the presence of sufficient cover of the right type for trout, and the presence of satisfactory conditions for feeding. All these factors are directly influenced by the velocity of the water, and this is determined not only by the gradient but also by the volume of water flowing. With increasing volume a decreasing gradient is required to produce a given velocity. Hence a given set of biologically significant conditions tends to be associated with decreasing gradients as the volume of the stream increases. This effect probably accounts for the difference between the gradients recorded by Hobbs in the lower reaches of the major South Island rivers and those found in the relatively small Horokiwi. It should be pointed out that the lower reaches of the Horokiwi, which have a mean gradient of 8.3 per 1,000, are similar to the South Island rivers in that they have a gravel bed and pass through a readily erodible flood-plain.

Although the rivers studied by Huet are of large size—the Semois is 210.5 km. (131 miles) in length—the trout appear to be largely restricted to the upper reaches and in most cases the "zone à truite" is less than 10 km. (6.2 miles) in length. This is about the same as the length of the Horokiwi and it is probable that in those parts of the river the volume of water is much more similar to the Horokiwi than to the big rivers mentioned by Hobbs. Comparison between the New Zealand and Belgian waters is however complicated by the much more diverse fish fauna of the latter. The waters examined by Huet contained thirteen species of fish in addition to trout, and, while some of these are characteristic of the lowest and most slow-flowing parts of the rivers, others, such as the grayling (*Thymallus thymallus* L.), the chub (*Squalius cephalus* L.) and the barbel (*Barbus barbus* L.), overlap with the trout to a considerable extent. It is not impossible that the absence of such species as these allows trout to establish themselves more abundantly in the quiet reaches of New Zealand rivers than they could otherwise do.

3. FLOW AND FLOODS

Unfortunately neither measurements of flow nor continuous or even daily records of water-level were available for the Horokiwi at the time of the investigation. The data which are available are of three types:

(*a*) Measurements of water-level in the Road and Back Branches at points not far above the junction, and in the Main Water at a point about half-way along its course, taken every time the stream was visited.

(*b*) Estimation of the maximum water-level of some floods by examination of the banks shortly afterwards.

(c) Daily rainfall records at Plimmerton at a point between the lower valley of the Horokiwi and the sea-coast.

The rainfall records, which were kept daily, provide the best indication of the probable nature of flow variations in the Horokiwi. As the recording point lies outside the drainage area it is however possible for significant discrepancies to occur, and one such instance was observed during the period of the investigation. On 21st June, 1939, very heavy rain fell for a time in the upper part of the drainage area, producing a rise of approximately 2 ft. 6 in. in both parts of the stream. The rainfall at Plimmerton on this day was only 0.53 inches and a rainfall of this amount would not normally produce nearly such a large rise in level.

TABLE 14. Comparison between rainfalls at Plimmerton and known resulting rises in level in the Horokiwi.

Date.	Rainfall (in.)	Rise in Level (in.).
21 June, 1939	0·53	30
25 August, 1939	3·00	19
21 November, 1939	0·10	9
28/29 February, 1940 ..	1·09	12
29 September, 1940	0·12	1·25
7 October, 1940	0·55	6·25
13 February, 1941	3·10	36
9 July, 1941	1·67	18
2 October, 1941	3·02	42

In the Horokiwi the most important variations in water-level from the biological aspect are those in which the rise is sufficiently great to produce a destructive flood, which may exert considerable influence on the trout population through movements of the stream bed, leading to destruction of the bottom fauna and disturbance of redds. It was therefore necessary to find out how far the occurrence and size of floods could be deduced from the rainfall data. Table 14 shows the recorded rainfall in the preceding 24 hours at Plimmerton for a number of rises of water-level of determinable height. Apart from the widely aberrant point which has already been referred to an unexpectedly close relationship appears to exist and indicates that a given rainfall at Plimmerton will produce a rise about 12 times as great in the level of the Horokiwi.

Observations of the effects of floods of various magnitude indicated that for use in this work the following classification of floods and their associated rainfalls would be suitable:

Type.	Rise in level.	Rainfall.	Extent of disturbance.
Slight	12–23 in.	1.0–1.99 in.	Some movement of surface gravel.
Moderate	24–35 in.	2.0–2.99 in.	Extensive movement of surface gravel with some movement to a considerable depth in regions of low stability; some changes of course; occasional bank erosion.
Severe	36 in. and over	3.0 in. and over	Widespread disturbance of gravel to a considerable depth; many changes of course; frequent bank erosion.

The extent of the erosion is controlled by other factors besides the magnitude of the rise in water-level. The duration of the period of high level has a decided effect on the extent of the disturbance, while the previous history is also of importance. When the gravel of the river bed has been disturbed by a flood it is for a time very loose and unstable, but it gradually becomes firmer and more consolidated. As a result, a flood which occurs shortly after another, while the bed is still in an unstable state, will cause much greater disturbance than one of identical characteristics occurring when the bed has become consolidated after a long period of low levels.

TABLE 15. The occurrence of "slight," "moderate," and "severe" floods, as determined by rainfall at Plimmerton during 1939-41.

Year.	Type of Flood.	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Total.
1939	Slight	1	..	..	1	..	..	..	3	..	1	..	2	8
	Moderate	..	..	..	..	..	1	..	..	..	..	..	..	1
	Severe	..	..	..	..	..	..	..	..	..	..	..	..	0
1940	Slight	1	..	..	..	..	..	1	..	..	..	..	1	3
	Moderate	1	..	..	..	..	..	..	..	..	..	..	..	1
	Severe	..	..	..	..	..	..	..	..	..	..	..	..	0
1941	Slight	1	2	1	..	..	1	2	1	1	2	..	..	11
	Moderate	..	..	..	..	..	..	1	..	1	..	..	..	2
	Severe	..	1	..	..	..	..	..	..	..	1	..	..	2

Table 15 shows the number of occurrences of each class of flood in each month of the years 1939–1941. These figures are based on the daily rainfall, but the two severe floods, as well as some of the lesser ones, were also recorded by direct observation. The moderate flood in June, 1939, is the one already mentioned which occurred without a correspondingly heavy rainfall at Plimmerton. The table shows clearly that conditions in 1941 formed a decided contrast with those of the two preceding years. This contrast is also shown by the total rainfall recorded at Plimmerton in each of the three years.

1939	38.61 inches
1940	41.70 inches
1941	57.59 inches

In the two preceding years, 1937 and 1938, the rainfall was very similar to that of 1939 and 1940; 1941 therefore showed an abrupt change from conditions which had become temporarily stabilized. As will be shown later, this produced physical

PLATE III. The lowest part of the Road Branch, which forms Zone II R, presents conditions which are essentially very similar to those in Zone II M, although on a smaller scale.

PLATE IV. In the lower part of Zone III, of which this view is typical, the valley walls are covered in bush, and the stream is flowing partly under the trees and partly through small grassy glades. The water is generally rapid and fairly shallow; the banks are stable and, in some places, are high and steep.

changes in the stream which had very pronounced effects on the trout population. During the eighteen years, 1931 to 1948 inclusive, for which rainfall records are available, conditions approximately similar to those of 1941 occurred in 1936 and 1947, while somewhat similar, but less severe, conditions occurred in 1943 and 1946.

Some of the 1941 floods recorded in Table 15 have special features which should be mentioned. The two "slight" floods in February occurred on the 12th and 14th, i.e., the days preceding and following the "severe" flood on the 13th; thus, in actuality, a single heavy flood occurred, produced by a rainfall of 5.92 in. spread over three days. Local reports described this flood as having its peak maintained for an exceptionally long period and this caused the amount of disturbance to be exceptional, even for a flood of such high peak. As a result the stream bed became unstable and moved exceptionally freely in the succession of smaller floods later in the year. These smaller floods occurred at sufficiently frequent intervals to maintain this state of instability.

One of the "slight" floods in July occurred on the day following the "moderate" flood of the 24th, giving a total rainfall for the two days of 3.10 in. One of the "slight" floods in October occurred on the 1st, the day preceding the "severe" flood, the rainfall for the two days being 4.57 in. Thus, although the number of distinct peaks was fewer than Table 15 suggests, the major floods were of greater magnitude. In addition to the definite floods, there were in 1941 a number of long periods of rain. These occurred particularly in the months of July and August when there were periods of 6, 8, and 15 days in which rain fell every day, the recorded rainfall for these periods being 2.11, 3.51, and 3.74 in. respectively. The long continued high levels produced by these rain periods tended to maintain the unstable conditions produced by the major floods. There were no rain periods in 1939 or 1940 which equalled the two major ones of 1941 either in duration or in total rainfall.

4. TEMPERATURE

Water temperatures were recorded whenever opportunity offered at the following points:

(*a*) A point at about the centre of the Main Water, close to the boundary between Zones I and II.

(*b*) On the Main Water just above the influence of the tide, and close to the road bridge.

(*c*) On the Back Branch near the road bridge and about 500 ft. above the junction.

(*d*) On the Road Branch about 4,500 ft. above the junction, and just below the point where the narrow valley commenced to open out.

Temperatures were generally read between 9.00 and 10.30 a.m. and, when readings were made at all four points, the observations were generally made within a period of about half an hour. When circumstances did not allow the four points to be visited, the observations were usually limited to the first point only, and consequently there are considerably more data for this than for any of the others. Owing to the irregular nature of the observations the results for the three years, 1939, 1940 and 1941 have been combined and Table 16 shows

the number of observations and the mean reading at point (*a*) for each calendar month. The extreme temperatures recorded at this point were 21.3° C. on 19th December, 1940, and 5.5° C. on 2nd July, 1941. The temperature of the Horokiwi falls well within the range which is suitable for brown trout. Thus Pentelow (1939) found that the growth of brown trout in experimental tanks was at a maximum between 50° F. (10° C.) and 60° F. (15.5° C.); while Brown (1946) found that growth rate was highest at about 7° C. and 19°C. and that although it fell slightly between these temperatures it fell much more rapidly above and below this range. Needham (1938) gives 81° F. (27.2° C.) as the limiting high temperature for this species, and further states: "Brown trout reach their best development in warmer streams showing maximum daily summer temperatures between 70°F. (21.1° C.) and 80° F. (26.7° C.)."

TABLE 16. The monthly mean temperature (°C.) and number of readings taken in each month at observation point (*a*) near the centre of the Main Water.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Number of readings ..	7	10	5	10	32	23	23	8	10	19	13	9
Mean temperature ..	19·5	16·9	16·2	12·8	11·2	8·2	7·5	10·2	11·5	13·6	16·0	17·9

The differences in observed temperatures at the various points were slight on any given day but did show certain consistencies despite the comparatively small number of readings. The two-monthly mean differences between the temperatures at each of the three remaining points and at point (*a*) are shown in Table 17. The ranges of difference for the three points are: (*b*) —2.2 to +0.9° C.: (*c*) —1.3 to +0.9° C.: (*d*) —3.3 to +0.2° C. It is apparent that while the temperatures at (*a*) are slightly higher than those at the mouth (*b*) and on the Back Branch (*c*) respectively, they are very distinctly higher than those recorded at (*d*) on the Road Branch. This result is not due to differences in time of observation, not only because of the relatively short period occupied by all four readings, but also because the two points of lowest temperature (*c*) and (*d*) were almost invariably visited after (*a*) and (*b*) and would for this reason be expected to give the highest figures since the readings were made while the temperatures were rising during the morning.

TABLE 17. The two-monthly mean temperature differences between observation point (*a*) and the other three observation points.

	Jan.–Feb.	Mar.–Apr.	May–June.	July–Aug.	Sep.–Oct.	Nov.–Dec.
Number of readings	10	12	37	17	18	13
Mean difference at (*b*)	−0·14	−0·47	−0·37	−0·64	−0·30	−0·23
Mean difference at (*c*)	−0·71	−0·56	−0·25	+0·01	−0·66	−0·58
Mean difference at (*d*)	−1·30	−1·35	−0·54	−0·78	−1·30	−1·94

There is however a very distinct correlation between the temperature characteristics and the nature of the stream and the surrounding valley in the region immediately above the observation points. These have already been discussed in detail, but the salient features may be summarized as follows:

(*a*) Valley wide and open; stream open, largely shallow, with pools few and small.

(*b*) Valley wide and open; stream somewhat entrenched with frequent deep pools.

(*c*) Valley open, but narrower than above; stream deeply entrenched in places, but often open; pools frequent but small.

(*d*) Valley narrow; stream largely overhung with trees; pools frequent but small.

When it is considered that these points are set out in descending order of observed temperatures, it is apparent that this is also the probable order of susceptibility to rises in temperature, since it clearly represents a descending order of exposure to sunlight and of contact between the water and circulating air. It appears very probable therefore that the observed temperature differences arise from differences in the rate at which the various parts of the stream warm up after the low night temperatures. If this is the case there should be corresponding differences in the daily range and possibly in the seasonal range in the various regions. That there is such a variation in the seasonal range is shown by the fact that the differences in the temperature readings between the exposed lower waters and the sheltered upper waters are clearly greater in the summer than in the winter months.

5. CHEMICAL FEATURES

(a) Composition of Water

No analyses for the estimation of dissolved substances were made during the time when the main part of this study was in progress. In order to provide some indication as to the chemical conditions in the stream, analyses were carried out on a series of samples taken in various parts of the stream on 1st February, 1951, when the stream was at normal summer level. Only slight differences were recorded for different parts of the stream, and the average values obtained were:

pH	6.9 (using Bromo-thymol blue as indicator)
Carbonate hardness	30.0 mg./l. $CaCO_3$
Nitrate	0.30 mg./l. NO_3
Silicate	16.0 mg./l. SiO_2
Phosphate	0.18 mg./l. P_2O_5
Dissolved oxygen	8.8 mg./l. O_2

The amount of phosphate present seems to be somewhat high, and this may be due to the topdressing of the drainage area with superphosphate on an extensive scale. If this is the cause it is not unlikely that the amount of phosphate present in solution may have been greater in 1951 than in 1939–41.

(b) Pollution

In the specification for a suitable stream for this work it was stated that there must be "no dangerous pollution." This condition was fully achieved in practice, and at no time during the period of the investigation was any pollution harmful to the fish stock observed in the Horokiwi. At a few points where houses lie close to the stream bank a certain amount of general domestic refuse has been thrown in from time to time, but never in amounts sufficient to have any biological effect outside the immediate locality. The only regular source of pollution was the

milking-shed and cowyards situated on the east bank of the Main Water immediately below the gorge section about 1,400 ft. below the junction. The manure and washings from these were regularly dumped on the bank of the stream in such a position that they drained into the stream, and a certain amount of solid matter was also washed in. After long periods without a fresh this caused the bottom of the stream to become blanketed for a distance of a few yards with insoluble fragments from the manure; this effect was however only temporary, and there was no evidence that the more or less continuous seepage from this dump was in any way harmful to the trout.

6. SUMMARY

The Horokiwi is a stream about 10 miles in length which divides into two equal branches about 3¼ miles from its mouth.

The lower part lies in an open alluvial valley, while the upper reaches are in a narrow valley between steep hills rising to 1,400 ft.

The drainage area is almost entirely in grassland.

Brown trout were introduced in 1884 and were well established by 1888. Since 1923 regular liberations of fry, averaging about 15,000 a year, have been made.

A physical survey of the stream was carried out by dividing it into a series of homogeneous sections, each belonging to one of the following types: Deep pool, pool, flat, run, stickle, and cascade.

The principal dimensions and features of each section were recorded, and provided the essential data regarding the area, length and characteristics of the major portions of the stream.

For analysis for this and other purposes the stream was divided into six zones, the principal characteristics of which are given in Tables 6 to 13. Although the boundaries of the zones were originally fixed by reference to the rate of growth of the trout, they are found to correspond closely to the physical features of the stream.

Pools were smaller and less numerous in the unstable zones, II M and II R, than in the more stable zones above and below this area.

The bed consisted predominantly of shingle. The size of the individual stones was greatest in the three lowest Road Branch zones, II R, III, and IV; it decreased downstream in the Main Water and was also less in the alluvial basin of Zone V at the top of the Road Branch.

Cover consisted mainly of temporary cover formed by marginal grass and cress, which was most abundant in the zones with much shallow water, and permanent cover formed by overhanging banks, logs, etc. This was generally abundant where there was much deep water.

Apart from local irregularities the gradient decreased steadily downstream from 17 per 1,000 to about 5 per 1,000.

In 1939 and 1940 rainfall was relatively slight and no significant flooding took place; in 1941 frequent heavy rain led to numerous floods which were particularly severe in February and October. These floods caused great disturbance of the stream bed, especially in Zone II M.

Recorded temperatures varied between 5° C. and 21° C. and there was little variation between the different parts of the stream; thus at almost all seasons the whole of the Horokiwi lies within the optimum temperature range for brown trout.

The concentrations of a number of dissolved substances found in a single series of analyses are listed on page 35.

There was no obviously harmful pollution of the stream at any time, although at one point cowyard drainage was regularly entering the stream.

PART III

The Environment—Biological

1. BOTTOM FAUNA

(a) Objects

The basic object of the present investigation was the study of the quantitative relationship between a trout population and its environment, especially its food supply. It was found that much the most important source of food of the trout of the Horokiwi was provided by the insects and other invertebrates of the bottom fauna. It was therefore essential to undertake a quantitative study of the bottom fauna in order to determine its relation with the amount actually eaten by the fish. This study had to include investigation of the fauna under different types of stream and bed conditions, in different regions of the stream, and at various times of year. It was necessary to determine not only the density of the fauna under all conditions, but also its specific composition, since, as is now generally realized, trout do not feed indiscriminately on all the animals of the bottom fauna, but tend to concentrate on particular species, either on account of their greater availability, or as a result of selection (Allen, 1942). The data had therefore to be in a form which would allow separate comparisons between the density of the fauna and the amount taken as food to be made, not only for the bottom fauna as a whole, but also for each species or group of species.

(b) Methods

As the object of this phase of the work was to estimate the total quantity and the distribution of the various components of the bottom fauna, it had to be based on an efficient system of sampling. The samples must be so distributed as regards position, water and bed type, and time, as to yield data on the effect of all these variables. When the observations were being originally planned, five sampling stations were selected in the Main Water and five in the Road Branch, and it was proposed to concentrate as many of the routine observations as possible at these points. The parts of the stream chosen for these stations were each approximately 900 ft. in length, and each was selected as being typical of the region of the stream in which it was situated. The positions of the stations, which were denoted as Stations M I to M V on the Main Water, and R I to R V on the Road Branch, are shown on the map. It was found that time did not allow a full series of observations on the desired scale to be made in all ten stations, and the number of faunistic samples originally planned had to be halved. As a result, full series of observations were made only in Stations M II and M IV and R II and R IV, and half the normal number of samples was taken in M V and R V. The observa-

tion stations actually used were distributed between the zones already mentioned as follows:—

Zone	I	Station M II
Zone	II	Stations M IV, M V
Zone	III	Station R II
Zone	IV	Station R IV
Zone	V	Station R V

Preliminary series of observations were made in September and December, 1939, and in January, 1940. In April, 1940, a series of 19 collections was made; of these collections, 6 were in M II, 7 in R IV, and 6 in R V. Thereafter a series of 20 collections was taken every two months until April, 1941; the distribution of these collections was 4 each in M II, M IV, R II and R IV, and 2 each in M V and R V. A final series of 2 collections each in M II, M V, R IV and R V was taken in October, 1941. In the stations in which four collections were made, one was taken in each of the four main water types, i.e., pool, flat, stickle and run. Where only two collections were made these were taken in flats and stickles.

The standard collection was 1 sq. ft. in area, and was taken by lifting from the stream bed, by means of a scoop, a sample measuring 12 in. x 12 in. The scoop used for this purpose was similar to that already described (Allen, 1940), and consisted of a heavy blade, 12 in. wide, behind which was a frame which carried an inner bag of stout twine netting (2 in. mesh) and an outer bag of fine canvas. A metal hood directed everything disturbed by the blade into the net when the apparatus was faced upstream. The blade of the scoop was pushed into the gravel of the stream bed to a depth of about 3 in. by means of a stout wooden handle, and the scoop was then forced upstream for 12 in. by one operator pushing on the handle and another pulling on a rope attached to the front of the scoop. Care was taken to ensure that none of the animals dislodged by the feet of the upstream operator were swept into the scoop. The resulting sample of gravel was washed in the field between two sieves of $\frac{1}{2}$ in. mesh and 1/30 in. mesh. The material retained between these, which included all but the most minute invertebrates, was carried back to the laboratory in hessian bags in a tank of formalin (4 per cent. formaldehyde).

At the laboratory the collections were washed in a stream of water in a wooden trough 4 ft. long and 8 in. wide; the light material including most of the animals was washed down into a sieve of 1/30 in. mesh. The heavier animals, such as the Trichoptera larvae with sand cases, were picked out of the gravel while it was in the trough. The light material was then spread in a shallow white enamel dish and sorted visually. The animals were removed by means of a pipette which obtained continuous suction from a filter pump, which contained a filter of fine bolting silk to retain the animals. The collection was then transferred to the counting apparatus; this consisted of a celluloid trough, $\frac{1}{2}$ in. wide and 8 in. long, drawn slowly along rails by an electric motor, the speed being controlled by a foot-operated rheostat. The animals were sorted into species, or, where desirable, larger groupings, by transferring them to appropriate tubes, and were at the same time recorded either on a set of cyclometer counters or on a writing pad.

In the principal groups, such as Ephemeroptera and Trichoptera, identification was taken when possible to the generic level, although in the latter order, where the larvae have been very inadequately described, it was often found necessary to group them into recognizable types within each family. In most other groups identification was usually taken as far as the family.

As it was proposed to study the gravimetric as well as the numerical relationship, all collections were weighed, the individual species or groups being treated separately. After draining off all surplus water on a pad of cotton wool, the animals were dried for three days at a temperature of 65° C. before weighing. It was found experimentally that this was sufficient to dry the samples to a constant weight.

The apparatus and procedure described above are essentially those which had been previously used by the writer in studying the relation between the bottom fauna and the food of the Atlantic salmon (Allen, 1940).

In order to be able to convert the data derived from the dry weights into approximate live weights, a conversion factor had to be determined for each of the principal forms. This was done by taking several samples, generally of 6 to 20 individuals of each type of approximately uniform size, drying them carefully between filter-papers, weighing them, drying by the standard method, and then re-weighing. In this way several determinations were made for each form and an average working value was selected.

The cased Trichoptera and the molluscs were removed from their shells or cases, and the animal and the shell or case were treated separately. In this way a factor was determined for conversion from the dry combined weight to the wet weight of the animal alone, since this is the significant factor when considering the fauna as a source of food. Difficulty was found in removing *Potamopyrgus* from its shell while retaining both shell and animal intact for weighing. The calcareous material of the shell was therefore removed by solution in hydrochloric acid, and a conversion factor determined by comparing the relative dry and wet weights of shelled and shell-less animals. The material used for the determination of these conversion factors had been preserved in 4 per cent. formalin for variable periods before use, and it is therefore possible that the results obtained might differ slightly from those obtainable from fresh material.

(c) Results

1. Numerical.—The results obtained by counting and weighing the collections referred to in the preceding section actually provide only a description of the fauna of the particular square-foot areas of stream bed which were sampled. For the purposes of the present study, it is necessary to draw from these results conclusions as to the fauna in all parts of the stream at all times during the period of the investigation.

Table 18 shows the number of each of the principal forms recorded in the entire 162 collections taken during the investigation. It will be seen that these forms made up 99.23 per cent. of all the animals recorded, and it was therefore

decided to concentrate the analysis of the results upon these forms and to ignore the remainder. Of the forms not considered only the crustacean *Paracalliope* and the larvae of one species of the Trichoptera appear to be of any significance in the food of trout.

TABLE 18. The numbers and percentages of the principal identified forms in the combined results of the 162 quantitative collections of the bottom fauna taken in the Horokiwi.

		Number.	Percentage.
Helicopsyche		20,496	*33·83*
Chironomidæ larvæ	7,201		
,, pupæ	1,415		
		8,616	*14·22*
Deleatidium		8,252	*13·62*
Parnidæ larvæ	7,910		
,, imagines	90		
		8,000	*13·20*
Pycnocentrodes larvæ	4,514		
,, pupæ	127		
		4,641	*7·66*
Sericostomatidæ—			
Type " C " larvæ	2,980		
,, pupæ	262		
		3,242	*5·35*
Potamopyrgus		2,896	*4·78*
Olinga larvæ		974	*1·60*
Hydropsyche larvæ	875		
,, pupæ	8		
		883	*1·45*
Rhyacophilidæ larvæ	355		
,, pupæ	176		
		531	*0·88*
Coloburiscus		407	*0·66*
Other Diptera larvæ		296	*0·49*
Oligochaeta		293	*0·48*
Latia		220	*0·36*
Simuliidæ larvæ	167		
,, pupæ	52		
		219	*0·36*
Leptoperlidæ		174	*0·29*
Others		449	*0·74*
Grand total		60,583	*99·97*

In order to make the best possible estimates of the density and composition of the fauna of the various parts of the stream at various times, the data obtained

from the samples have been analysed to determine the trends which affect each of the forms involved. Variations have been considered with respect to three environmental factors; these were water type, zone and season. It has been frequently shown that the depth, velocity and nature of bed all have pronounced effects on the density and composition of the bottom fauna of a stream. Water type, in the sense in which it is used in this study, is a function of the first two of these factors, and it has also been shown that, to a great extent, the water type and the zone together determine the nature of the bed. Thus, an analysis based on water type and zone actually allows for the effects of the more fundamental factors, and gives results which can more conveniently be applied to the determination of the fauna both of the stream as a whole and of the separate zones. Knowledge of the individual nature of the fauna of the separate zones is essential for comparison of the different characteristics of their trout stocks and food supplies. Changes in the fauna from time to time are caused both by normal seasonal variations due to the life histories of the various animals, and by special effects such as the floods of 1941 which led to substantial destruction of the bottom fauna in certain parts of the stream.

In order to determine the major trends in relation to water type, the mean number of each form per sample has been calculated for each water type, regardless of zone or time. These figures have then been expressed as a proportion of the mean of the four densities, the results being shown in Table 19. These show clearly the differences in the characteristic habitats selected by the various forms; thus, the Leptoperlidae and Sericostomatid type "C" and *Coloburiscus* show a decided preference for rapid water, while at the other extreme such forms as Parnidae larvae, *Potamopyrgus* and the Oligochaeta occur predominantly in quiet water. A few forms like *Deleatidium* show relatively uniform distribution, though most of them show some degree of preference for a particular water type. Although these results are based on series of collections taken at various times and in various parts of the stream, the differences between the water types are sufficiently pronounced and, when worked out separately, are sufficiently consistent for the different zones, to leave little doubt as to the significance of the results. In some cases the results suggested that when an animal was scarce it was more uniformly distributed than when it was abundant, since the differences between the water types were more pronounced in the latter case. The significance of this effect has however not been tested statistically.

In order to study the trends arising from differences in position and time, comparisons have been based on the mean of a series of four samples, one being taken in each of the four water types, stickle, run, flat and pool. Series of this composition were actually taken in stations M II, M IV, R II and R IV on all dates between June, 1940, and April, 1941. In the December, 1939-January, 1940, and the April, 1940 series, more than one sample was taken from some of the water types at some stations. In these cases the mean for each water type was calculated for each station, and the station mean was then determined from these. All samples from stations M V and R V after April, 1940, and from stations M II, M V, R IV and R V in October, 1941, were taken only in stickles and flats. In these cases the station mean has been adjusted by multiplying it by the reciprocal of the mean of the relative densities for stickles and flats shown in Table 19. Application

TABLE 19. Factors affecting the distribution of the principal types identified in the bottom fauna.

	Relative Densities for Stream Types.				Relative Densities in Zones.					Correction Factor for Zones.					Dr-wt. : wet-wt. Conversion Factor.
	Stickle.	Run.	Flat.	Pool.	I.	II.	III.	IV.	V.	I.	II.	III.	IV.	V.	
Hydropsyche	1·34	1·34	0·82	0·50	1·44	0·98	0·63	0·82	1·14	0·93	1·12	1·01	1·05	1·05	3·6
Rhyacophilidæ larvæ	0·98	0·79	1·26	0·98	0·80	1·44	1·05	0·63	1·08	1·05	1·04	1·08	1·05	1·07	4·5
,, pupæ	1·60	1·00	1·20	0·20	1·19	1·66	0·79	0·55	0·82	1·04	1·32	1·20	1·23	1·25	4·5
Helicopsyche	0·61	1·18	0·92	1·28	0·04	0·46	1·38	1·78	1·34	0·93	0·80	0·86	0·84	0·84	0·43
Olinga larvæ	0·68	0·31	1·20	1·81	0·31	0·71	1·22	0·90	1·86	1·16	0·90	1·05	0·99	0·99	1·2
Sericostomatidæ															
Type " C " larvæ	2·57	0·86	0·51	0·06	0·08	0·91	1·68	1·85	1·48	1·14	1·67	1·32	1·46	1·41	0·50
,, pupæ	2·21	1·31	0·48	0·00	0·18	1·26	0·79	0·84	1·92	1·00	1·48	1·16	1·29	1·25	0·50
Pycnocentrodes larvæ	0·80	1·20	1·43	0·56	0·82	0·74	1·81	0·23	1·40	0·94	0·98	1·02	0·98	1·03	0·66
,, pupæ	0·82	2·71	0·23	0·23	2·68	1·75	0·18	0·00	0·26	0·54	0·74	0·57	0·65	0·63	0·66
Coloburiscus	2·06	1·38	0·43	0·13	1·03	1·15	0·60	0·80	1·42	0·97	1·40	1·10	1·23	1·19	3·9
Deleatidium	0·88	0·72	1·14	1·27	1·12	0·85	0·60	1·09	1·34	1·07	0·97	1·03	1·01	1·01	4·3
Leptoperlidae	3·22	0·33	0·22	0·22	0·16	0·21	3·78	0·34	0·51	1·31	1·95	1·48	1·68	1·60	3·7
Parnidæ imagines	1·22	1·04	0·35	1·39	2·59	0·45	0·64	0·73	0·59	1·00	0·99	0·91	0·97	0·91	2·0
,, larvæ	0·26	0·40	0·93	2·40	2·97	0·76	0·49	0·12	0·66	1·11	0·65	0·87	0·81	0·77	2·0
Chironomidae larvæ	0·94	0·57	1·50	0·99	1·39	2·93	0·14	0·38	0·16	1·11	1·07	1·15	1·10	1·13	3·7
,, pupæ	0·85	0·52	1·59	1·04	1·23	3·25	0·06	0·28	0·18	1·12	1·04	1·15	1·09	1·13	4·8
Simuliidæ larvæ	1·66	1·95	0·29	0·10	1·86	2·82	0·12	0·03	0·17	0·79	1·17	0·90	1·01	0·98	4·2
,, pupæ	1·85	1·23	0·61	0·31	2·21	2·66	0·13	0·00	0·00	0·99	1·33	1·10	1·20	1·17	4·2
Other Diptera larvæ	0·76	0·86	1·08	1·30	1·03	1·02	0·62	0·85	1·48	1·02	0·90	0·97	0·95	0·95	3·5
Potamopyrgus	0·13	0·89	0·68	2·30	2·95	0·58	0·38	0·34	0·75	0·97	0·53	0·71	0·67	0·64	1·9
Latia	1·16	0·44	0·65	1·75	0·10	0·03	2·56	1·47	0·84	1·16	1·03	1·03	1·06	1·01	1·15
Oligochaeta	0·34	0·39	0·78	2·49	2·80	0·70	0·09	0·22	1·20	1·12	0·66	0·86	0·81	0·77	3·8

of this correction gives for each station the mean density which would have been obtained from a full series of four collections if all forms had been distributed between the water types in the typical way. The tables in Appendix I show the mean number of each form taken at each station on each collection date, adjusted as above where necessary.

Study of the distribution of each form in relation to the different zones of the stream has been based primarily on the four series of samples taken between June and December, 1940. In all of these full series were obtained on each date, except that sampling at stations M V and R V was restricted to flats and stickles. During this period there were no significant disturbances of the fauna by outside factors such as floods. Except at the end of the period variation due to internal causes such as the emergence of adult insects would also be at a minimum. The results were then smoothed by the following method to show the zonal and seasonal trends while eliminating to some extent the variation due to sampling errors. For each form a table was constructed by entering the date-station means in horizontal lines for each station and vertical columns for each date. The sums of each line and column and the grand total were then determined. The product of the sums for the line and column intersecting there, divided by the grand total, was then entered in each square. These smoothed means then give for each station a series of densities which vary with date in accordance with the average for all stations; and for each date, a series corresponding with the average station variations. In order to show the effect of the zonal distribution, Table 19 shows for each form the smoothed mean density in each zone in relation to the mean for all zones. For the December, 1939–January, 1940, and the April, 1940 series no data were available for Stations M IV, M V and R II, but there was no reason to suppose that the distribution in respect to stations at those times differed significantly from that occurring in the later part of 1940. Values were therefore computed for these two dates which gave the actual mean density and the same relative densities as those found by the method described above for the three stations sampled.

The severe flood of 13th February, 1941, greatly reduced the abundance of bottom fauna on account of the disturbance of the stream bed which took place. The extent of the disturbance, and therefore of the destruction of the bottom fauna, varied greatly in different parts of the stream, largely on account of differences in the stability of the bed. The relative distribution of the fauna in different parts of the stream was therefore very different after the flood from that for 1940, and the average distribution figures used in 1940 could not be used in 1941. Full series of samples were however obtained in February (after the flood) and April, 1941. The results for these two months were therefore smoothed by the same methods as were used for the data for June to December, 1940. For October, 1941 estimates were made for those stations for which no direct data were available by inserting values which bore the same relation to the mean for the stations sampled as was found in February and April, 1941. Since the analysis has been carried out on a zonal basis, and Zone II includes Stations M IV and M V, all results for Zone II have been based on the mean for the two stations.

The methods described have yielded means for each zone which give equal weight to each of the four main water types. It has however been shown in Table 7 that the proportions of the different water types vary considerably from zone to zone. In order to make an estimate of the average fauna of the whole zone, it is necessary to make allowance for this effect. For this purpose a correction factor has been computed for each form in each zone by multiplying the relative density for each water type by the proportion of that water type in the area of the zone, and by adding the products. For this purpose deep pools have been included with pools, and cascades with stickles. Results for Sub-zones II M and II R have been combined, as no direct faunistic data were available for the latter. These correction factors are shown in Table 19 and it will be seen that they vary considerably for the different forms, both in their average value and in the extent of the differences between the zones. The average fauna over the whole of each zone has been estimated by multiplying the smoothed means discussed above by these correction factors and the results are shown in Appendix I as the *estimated fauna*.

The total estimated fauna has been obtained by adding the values for the component forms. This method of deriving the total fauna has been adopted since it is essential to have estimates of the density and distribution of each of the principal forms in the fauna. An alternative procedure would have been to have studied the trends of the total fauna and prepared smoothed estimates of its density, and then to have applied the same procedure to its proportionate composition. In addition to its complexity, this method would have been much less satisfactory, since the trends, both for the total fauna and for the proportion formed by any one part of it, would be the resultant of the trends shown by all the components, and could not therefore be handled by the comparatively simple methods described.

It is necessary to give consideration to the degree of reliability of the estimates of the fauna which have been prepared above. The estimation of stream-bottom faunas by means of sampling techniques, generally using 1 sq. ft. samples, has become a regular part of fisheries investigations, and many workers from Needham (1934) onwards have drawn attention to the amount of variation which may occur between apparently similar samples, and have been concerned as to the effect of these sampling differences on the reliability of the method. Needham (*loc. cit.*) examined the results of 10 collections, taken under apparently rather similar conditions, although in various streams. The results ranged from 0.65 gm. to 4.19 gm. total wet weight per sq. ft. His results show a mean of 2.06 gm. and a standard deviation of 1.28 gm. (62.2 per cent.). Subsequently Mottley, Rayner and Rainwater (1939), and Leonard (1939) undertook further studies of the problem. The former examined the results of 35 collections made under similar conditions by eight workers. These showed a mean of 161.9 animals per 1,000 sq.cm. and a standard deviation of 94.1 (58.3 per cent.). Further examination however suggests that there were considerable differences in the results obtained by different workers despite the similar method, and an analysis by means of probability paper (Harding, 1949) indicates that the collections belong to two approximately equal groups, one with a mean of 228 and S.D. 57.5 (25.2 per cent.), and the other with a mean of 78 and S.D. 45 (57.5 per cent.). Leonard (*loc. cit.*) appears to

have taken greater precautions to ensure that the areas sampled were as similar as was practicable, and, possibly as a consequence, his results show a higher degree of uniformity than those of the preceding workers. Analysis of two series of five and ten samples respectively show means of 893 and 800 animals per sq. ft. with corresponding standard deviations of 208 (23.2 per cent.) and 140 (17.5 per cent.). Leonard points out that the component species generally show a higher degree of variation than does the total fauna, and concludes that "one sample of the sort described may be depended upon to yield a reasonably accurate index of the amount of food organisms produced per unit area of uniform bottom, but cannot be expected to provide a comprehensive picture of the relative numbers of individual species throughout the larger areas from which the sample is collected." Examination of his data shows that in the two series of collections the standard deviation of five of the most common animals varies from 20 per cent. to 48 per cent. of the mean, and is thus distinctly higher than that of the total numbers in the collections. Mottley *et al.* (*loc. cit.*) found that the standard deviations for the various groups of insects in their collections were generally about 70 per cent. to 100 per cent. of the mean; this is noticeably higher than the value for the total numbers. Surber (1937) examined the variation in the occurrence of the most abundant animal, *Gammarus,* in three series containing 15, 17, and 16 samples of 1 sq.ft. each taken in successive months. He records "deviations" forming 26.2 per cent., 29.8 per cent. and 35.9 per cent. of the respective means.

The data available from the present studies are not generally suitable for examination of this question, since the scheme of collections was designed to provide data on the effects of such variables as water type, location and season. In a few instances, analysis of the effects of these variables has shown that a small group of collections might have been expected to contain substantially similar numbers of a particular animal. In such cases the degree of variation in the numbers actually recorded would provide an indication of the nature of the random sampling errors. This has been possible for *Helicopsyche* in 17 samples taken on the runs, flats and pools of Zones III and IV in June, August and October, 1940. These collections yielded a mean of 389 with a standard deviation of 275 (70.6 per cent.). The distribution was found to be strongly positively skewed and a more symmetrical distribution was found to be that of $\sqrt{\log_{10} n}$, where n was the number of animals in the collection. This gave a mean of 1.5829 with S.D. 0.0918. The corresponding values for n are mean 320, S.D. + 317 (99 per cent.) or — 153 (48 per cent.). For *Pycnocentrodes*, two separate series of 12 samples, taken in the stickles and flats respectively in Zones I and II between June and December, 1940, were found to be suitable for study. These gave relatively symmetrical distributions with means of 26.25 and 62.75 and corresponding standard deviations of 21.1 (81 per cent.) and 71.2 (113 per cent.). For *Delcatidium* nymphs, a series of 18 samples was examined from flats and pools for collections which gave smoothed values between 50 and 65. The actual mean was 64.0, and the corresponding standard deviation 30.4 (47.7 per cent.).

The general conclusion which emerges is that the standard deviation of the total numbers in a series of faunistic collections, taken by similar methods under similar conditions, usually lies between 20 per cent. and 50 per cent. of the mean, and that

the numbers of any particular form are generally distributed with a larger and more variable standard deviation, usually between 30 per cent. and 100 per cent. of the mean. As might be expected, smaller deviations appear to occur where greater care has been taken to standardize the conditions, and where the bottom is of a type which gives a relatively uniform habitat. A stream bed composed of rounded stones, which are small in proportion to the area sampled, will tend to give both less variation in the total surface area and more uniform conditions than will one composed of irregular stones which are large in proportion to the sampling area. The unusually low standard deviations for particular groups recorded in the data of Leonard and Surber appear to have been obtained on stream beds of this type; in both cases the predominant stones were said to be similar to hens' eggs. A relatively low standard deviation was also obtained in the Horokiwi for *Deleatidium;* these collections were made in quiet water and chiefly in Zones I and II, and it has already been shown that under these conditions the stream bed is normally composed of relatively small smooth stones.

These conclusions may be used to make an approximate estimate of the degree of reliability of the estimated faunas given in Appendix I. These estimates are based primarily on the means of the lines and columns of the table referred to above. The lines normally include 16 collections, although there are 24 and 8 in Zones II and V respectively, and the vertical columns 20 collections. If all the collections in a column or line were drawn from the same set of conditions, the limits of the population mean for any degree of probability can be determined by taking the appropriate value of t from a table and inserting it in the formula

$$\bar{x} - m = \frac{t\,s}{\sqrt{n}}$$

using the notation of Snedecor (1946). For the columns of 20 collections $t = 2.101$ for $P = 0.05$, and if the standard deviation (s) = 50 per cent. of the collection mean ($\bar{x}$), then the probable limits of the true mean (m) in relation to the collection mean ($\bar{x}$) are given by $\bar{x} - m = \pm\ 0.235\bar{x}$. In other words, there is only one chance in twenty that the actual mean for the population differs from the collection mean by more than 23.5 per cent. For lines of 16 the corresponding range is ± 26.8 per cent. Where the standard deviation is 100 per cent. of the mean the limits are correspondingly twice as great.

We have already seen that while the standard deviation for particular forms may range up to about 100 per cent. of the mean, it is also sometimes less than 50 per cent., particularly when precautions are taken to ensure uniformity of collecting conditions. These estimates of the limits of probable error are based of course on the assumption that all the samples in a column or line have been taken from populations which are identical in their mean density and in the distribution of the component forms. The method should however indicate the probable error in the estimate of the mean of the various populations from which the samples are drawn, provided that the populations are reasonably similar. The mean will of course be weighted in accordance with the distribution of the samples. Where however some of the samples are taken from populations which are much less

numerous than the others, these samples will have a correspondingly little effect on the collection mean. Consequently the mean is in effect based on a smaller number of collections, and has therefore a larger probable error. In view of these effects it appears that the estimated numbers of the various forms generally have a probable error of about ± 50 per cent. for $P = 0.05$. The estimates for the most evenly distributed forms are probably somewhat more accurate, and those for the forms concentrated in certain localities or types of water somewhat less accurate. Similarly it can be shown that for $P = 0.2$ the range of probable error is about ± 30 per cent. That is, that there are four chances in five that the estimates are within 30 per cent. of the true population mean.

A further source of error which might occur in the smoothing process lies in the assumption that the faunas of the various zones did not vary significantly in their relative densities within the periods stated. While no precise test of this assumption has been made, the detailed data suggest that it was generally justified, and that any errors introduced in this way would be small compared with the sampling errors. In the same way the consistency of the results obtained at different stations suggests that the errors due to variation in the relative densities in different water types were comparatively small, and in any case the correction factors derived from these do not as a rule differ greatly from one.

2. Gravimetric.—The mean individual dry weight of each form was determined for each group of samples taken at a particular station and date by dividing the total dry weight by the total number of individuals. The resulting values are shown in Appendix II. The reliability of the estimated mean will depend greatly on the size of the sample, and it may depart considerably from the true mean in some cases where the samples were small, and the variation in the size of the individuals was large. In an attempt to avoid major errors arising in this way, all values based on less than 10 individuals were carefully scrutinized, and if they appeared to diverge significantly from the values recorded for larger samples taken on similar dates and in nearby zones, they were replaced by approximate values based on the trends shown by the larger samples. Values were also estimated by comparison for those dates and stations which were omitted in the collection series (i.e., M IV, M V, and R II, in December, 1939–January, 1940, and April, 1940; and M IV and R II in October, 1941). In the table the estimated values are shown in italics, and measured values in roman type. Certain significant changes in mean weights, including those arising from growth and from differences between the zones, will be discussed in a later section of this paper.

From these mean dry weights, mean wet weights have been calculated by application of the conversion factors derived by the method described earlier and shown in Table 19. The mean wet weights have then been combined with the estimated numbers shown in Appendix I to give the estimates of total wet weight and percentage wet weight, which are shown for each form in Appendix II. The accuracy of these estimates is of course limited not only by that of the estimated numbers, which has already been discussed, but also by that of the estimates of mean wet weight. The estimates of mean wet weight will be subject to sampling errors in the collection of the animals on which the mean dry weight is based, and to systematic errors in the conversion factors. These systematic errors will in turn

PLATE V. The gorge-like nature of Zone IV is illustrated by this photograph which shows the very steep valley walls running straight down to the stream, and the virtual absence of any flood-plain. The slopes are generally covered with scrub, particularly gorse, which overhangs the stream in many places.

PLATE VI. Zone V, which is shown in this photograph, lies in a small open basin among the hills, and in many respects resembles Zones I and II rather than the part of the Road Branch below it. The observed part of the stream ended behind the wool-shed in the middle distance, where an important tributary enters from a steep gully on the left.

be liable to sampling errors since they were determined only for small samples of the population; they may also be subject to errors due to local variations or to changes during the life of the animal. Since, in each sample, all the individuals of each form were handled as a group, the data yield no information on the magnitude of probable sampling errors. Moon (1939), who studied the growth of two genera of Ephemeroptera, showed that for these forms, which had an annual life-cycle and a short clearly-defined emergence period, the variation in length is relatively small, the standard deviation generally being between 10 per cent. and 20 per cent. of the mean. Under such conditions the probable error of the mean of samples of 50 or more, such as are represented by many of the more numerous animals in the present collections, would be less than 5 per cent., and would therefore be small compared to the probable error of the estimated numbers. Certain groups show an abnormally wide range of individual size within single collections. This may occur where the group consists of more than one species or where the component forms have a life-cycle which is either short and non-seasonal or else lasts for more than one year. In such cases the probable error of the mean will consequently be increased, and may become large enough to cause the estimate of the total wet weight to be appreciably less reliable than that of the estimated numbers.

(d) Discussion

1. Specific Features.—In the preceding sections the fauna has been discussed as a whole, and the major component groups have only been listed. It is necessary however that the groups into which the fauna was separated should be more clearly defined, and in many cases there are points in connection with the life-cycle or distribution of these animals which require further examination, since they may affect the food supply available to the trout. The succeeding sections will therefore contain a definition of each group and a brief discussion of its ecology.

Trichoptera

Hydropsyche: This includes all larvae and pupae belonging to this genus, of which Tillyard (1924) has listed five species as occurring in New Zealand. It is not known however whether more than one species is present in the Horokiwi. This genus is much more numerous in stickles and runs than elsewhere, and is clearly a rapid water form; it appears to be relatively more common in open, stable sections of the stream.

There is no indication of any differences in average size in different parts of the stream, but changes due to the growth of the larvae are distinct. The average size is at a minimum about December, and thereafter increases steadily until August. It then remains almost constant until October, before falling sharply to the low December values. These stages clearly correspond to first a period of growth, then a period when most of the larvae are mature, and finally to the disappearance of mature larvae through emergence and the contemporaneous appearance of the next season's young larvae.

Only a few pupae were identified as belonging to this genus and these were taken in various months throughout the year.

Rhyacophilidae: About twelve different larvae belonging to this family were distinguished during the investigation, but as most of these occurred in fairly small numbers, and no striking differences in their distribution were apparent, they have been grouped together for the present purpose. It would in any case have been impossible to put either specific or generic names to these forms without undertaking extensive rearing work for which time was not available.

The distribution between the zones is somewhat irregular and, not unnaturally, follows the same general pattern for both larvae and pupae. This probably arises from the mixture of forms referred to above. Both larvae and pupae appear to show a preference for shallow water conditions, i.e., stickles or flats.

The proportion of pupae is at a maximum in spring and early summer, and the larvae seem to be at their maximum size at about the same time. This suggests that the emergence period of most of the species concerned is early summer.

Helicopsyche: Three species of this genus have been recorded from New Zealand (Tillyard, 1924), but specific identification of the Horokiwi forms was not attempted. The most striking feature of the distribution of this form is its abundance in the three highest zones where it was normally much the most numerous animal, and its scarcity farther downstream, particularly in Zone I. It is not confined to any particular types of water, but seems most frequent in the relatively deeper water of runs and pools.

This form shows well-marked differences in size in different portions of the stream. There is a progressive falling-off in size from Zone I upstream as far as Zone IV, and an appreciable increase in size again in Zone V. This occurs at almost all seasons. This size distribution suggested that there might be an inverse correlation between size and population density and it was therefore decided to investigate the matter further. For this purpose the relation between average size and number in the square-foot sample was examined in each of the four series of eight collections taken in Zones III and IV between June and December, 1940. In no case was any significant correlation found to exist. It appears therefore that even if the relatively small size of *Helicopsyche* in those zones in which it is most abundant is a result of the higher population density, the mechanism by which it operates is not such as to produce similar effects from point to point in any one part of the stream.

Further tests did however indicate that there was a direct relation between the weight of *Helicopsyche* and the type of water in which it was living. When numerical values were given to the four water types in descending order of current velocity, i.e., stickle = 1, run = 2, flat = 3, and pool = 4, determination of the correlation coefficients for the four series of eight samples mentioned above gave values of $r = -0.892$, -0.490, -0.976, and -0.454. The two highest values of r each have probabilities of less than 0.01. It appears therefore that *Helicopsyche* tends to be of larger size, at least as far as the dry weight of animal and case is concerned, in more rapid water. It follows that some correction for this effect should strictly have been made in estimating the weight of this form in each zone, but it seems likely that the error introduced in this way is small compared to the sampling errors already present, and the effect has therefore

been ignored. A similar variation in average size in relation to habitat has been shown by Lyman (1943) for the nymphs of the mayfly *Hexagenia*; in this case nymphs living in mud were larger than those living in a coarser substratum.

The data are not sufficient to show the actual causes of these differences in size in different environments. Possible causes include different rates of growth in different environments, changes in habits during the growth of the larvae, variation in the weight of the case due perhaps to differences in the available material, and the occurrence of two or more species of different size and different habitat requirements.

Olinga: This group is formed of the single genus, which is represented in New Zealand by a single described species, *O. feredayi*. As Table 19 shows, this is predominantly a quiet-water form and one which tends to become progressively more abundant upstream, although it is rather less numerous in Zone IV than in Zone III.

No distinct seasonal variations in the average size of the larvae were recorded; it is not however known whether this is because the life-cycle lasts more than one year, or because of the lack of clearly-defined seasonal effects in its life-history. The average weight of the larvae tends to become progressively less upstream, except that it is relatively larger in Zone IV than in Zone III.

Insufficient pupae of this species were taken to enable any conclusions as to their occurrence to be drawn.

Sericostomatid "C": This is an abundant and very distinct caddis, which, being known only in the larval and pupal stages, could not be placed generically. The most distinctive feature is the larval case, which, like *Olinga*, is composed entirely of horny material without any mineral or vegetable matter. It differs from *Olinga* in its smaller size (maximum length about 1 cm.) and in its proportionately greater width, and the strikingly oblique anterior opening. Table 19 shows that this is decidedly a rapid-water form, in both larval and pupal stages, being much more abundant in stickles than in water of any other type. Although it differs completely from *Olinga* in this respect, it resembles it closely in its distribution along the length of the stream: it becomes progressively more numerous upstream, apart from Zone IV where it is rather less abundant than in Zone III. It is however even more scarce than *Olinga* in Zone I.

The relative weights of this form in the different zones appear to follow the same general trend as that shown by *Helicopsyche*, although the range of variation is less pronounced.

In order to study factors which might affect the size of the larvae the results of the two series of eight collections taken in Zones III and IV in June and August, 1940, have been examined. The correlation with water type, such as was shown by *Helicopsyche*, gives values for r of -0.742 and -0.428, which may indicate a slight tendency for larger larvae to be found in more rapid water, although the level of significance is low. On the other hand, when the mean weight is compared with number of larvae in the sample, values of r of 0.868 and 0.934

are obtained. This indicates an increase in larval size with numbers, with a very high level of significance. Thus, it appears that in any particular part of the stream the larvae are largest where they are most numerous, although larval size seems to vary inversely with abundance in the stream as a whole.

The average size of the larvae is low during the early part of the year, increases rapidly between April and August as the larvae reach maturity, and remains high during the rest of the year when most of the larvae present are full-grown. The occurrence of pupae in relatively large numbers between August and December is in accordance with this.

Pycnocentrodes: Tillyard (1924) has described four species of this genus, and two of these, *P. chiltoni*, Tillyard, and *P. pulchella*, Tillyard, have been recorded from the Horokiwi. This larva has a rather broad case composed of fairly coarse sand grains, and reaches a maximum length of about 1.2 cm. This form shows a relatively uniform distribution, and is most abundant in the intermediate conditions offered by runs and flats. Its distribution along the course of the stream is somewhat similar to the two preceding forms, although the increase upstream is rather less pronounced, while the reduction in numbers in Zone IV is much greater.

The variation in size between the zones shows the usual tendency for a progressive reduction upstream, although in this case Zone III apparently produces the smallest larvae. The correlations between size and density, and size and water type, have again been examined. No indication of correlation between density and size was found, but the correlation with water type gave conflicting results. The series used were drawn from Stations R II and R IV; in June and August values of r of -0.558 and -0.054 were obtained, which are well below the significance level; on the other hand, the values in October and December were -0.838 and -0.766, both having a probability of chance occurrence of less than 0.05. This indicates that in the later part of the year the heavier larvae (dry weight including case) are found in the more rapid water.

Seasonal growth in this form is very pronounced. The mean weight is at a minimum from April to June and then rises steadily until December. There is then a steady decrease in late summer, which probably arises from a decrease in the number of mature larvae and an increase in the number of young larvae. The comparatively small number of pupae collected suggests that this stage is relatively short.

Ephemeroptera

Coloburiscus: *C. humeralis* (Walker) is the only species of this genus recorded from New Zealand (Phillips, 1930). As Table 19 shows this is a rapid-water form, and is fairly well distributed along the stream, although it appears to be most abundant in the open areas.

No distinct local variations in average size were found but there are definite seasonal changes. The nymphs are at a minimum size about April, and thereafter increase gradually in average weight to a maximum in October, after which there is a slow decrease to the April value. This decrease probably arises from the

gradual replacement of large mature nymphs by young ones and Phillips has noted that winged stages are present from the middle of October to the beginning of February.

Deleatidium: Under this heading are grouped the nymphs of all the mayflies belonging to the two closely related genera *Deleatidium* and *Atalophlebia*. In all, thirteen species of these genera have been recorded from New Zealand (Phillips, 1930) and several of these have been identified in the Horokiwi. Since however no attempt has been made to list all the species occurring there, or to study their specific characteristics, the group has been treated as a whole in the present work. It is probably a result of its multi-specific nature that the group appears to be unusually uniform both in its distribution along the stream and in its seasonal occurrence. This is the only group which is abundant in all parts of the stream, although, as Table 19 shows, it is rather less abundant in Zone III than elsewhere. It is also found freely in all water types, but is most numerous in the quieter waters of the flats and pools.

These animals show, although not very markedly, the general tendency to decrease in average weight upstream, but in this case the tendency continues right through to Zone V. The usual analysis of the correlation of size with water type and number in the sample has been carried out for this form. No correlation with number in sample was found, and the results for water type were inconclusive, although there was some indication that the average size may be greater in more rapid water.

Plecoptera

Leptoperlidae: Tillyard (1926) records 16 species of this family as occurring in New Zealand. No attempt was made to compile a complete list of the species occurring in the Horokiwi, or to study their specific biology, but the following species have been identified: *Zelandobius furcillatus*, Tillyard, *Nesoperla spiniger*, Tillyard, and *N. trivacuata*, Tillyard. Despite the fact that this group evidently consists of several species, it shows the most highly localized distribution of any of the important groups in the Horokiwi. Table 19 shows that it is virtually confined to the bush-enclosed waters of Zone III, and that even within this area it is largely restricted to the shallow rapid waters of the stickles.

Owing to this concentration in one part of the stream, no data are available as to whether there are any significant local variations in its size. The nymphs do however show well-marked seasonal changes in size, with a maximum in August and a minimum in late summer. These changes are very probably correlated with an emergence period in early summer. Tillyard (1923) records the capture of imagines of the three species listed above in November and January.

Coleoptera

Parnidae: The beetles of this family were represented in the bottom fauna by both larvae and imagines, although the former were very much more abundant and were found throughout the year, whereas the adults had a relatively short season. The species present were not identified, but the cylindrical nature of the larvae indicated that they belonged to the sub-family Dryopinae (Tillyard, 1926).

As Table 19 shows, these animals are very much more abundant in the lowest zone than in any of the higher zones, although the larvae seem to show a slight increase in Zone V. In the larval stage they are essentially quiet-water forms, and are found in much greater numbers in pools than in any other type of water. The imagines seem to be rather more evenly distributed.

Examination of the seasonal changes indicates that the larvae are least abundant and have their maximum weight in June, and that by August the numbers have abruptly increased to a maximum while the weight has declined sharply. Thereafter there is a steady decrease in numbers and increase in weight. These facts suggest that between June and August the majority of one generation of larvae have pupated, while the succeeding year-class has reached a size large enough to be taken by the methods used. Imagines were found to be relatively more numerous at mid-summer than at other times, and in December, 1939, were 3.6 per cent. as numerous as the larvae. There is comparatively little local variation in the larval size of these forms.

DIPTERA

Chironomidae: The larvae and pupae of this family were found in considerable numbers in some parts of the stream, but no attempt was made to carry their identification further. Tillyard (1926) states that 75 species are known from New Zealand. Table 19 shows these animals to have one of the most unusual distributions found among the bottom fauna of the Horokiwi. They are concentrated in Zone II and are found in distinctly reduced numbers both upstream and downstream from this area. Comparison of the results of collections taken at Stations M IV and M V shows that the centre is actually near to the former of these, i.e., in the lower part of Zone II, and that in the upper part of this zone the density is no greater than in Zone I.

Both larval and pupal stages are found most abundantly on the flats where the larvae form fine silken galleries on the tops of the stones. The larvae appear to undergo some seasonal changes in abundance, and to be most numerous in mid-winter. These changes seem to be most pronounced in the regions immediately above and below the centre of abundance. At the centre itself, and in the upper part of the Road Branch, fluctuations are smaller and the chironomid population tends to be more constant at high and low levels respectively. Pupae are present in fair numbers at all times and frequently are between 20 per cent. and 50 per cent. of the numbers of the larvae.

The larvae also appear to show the usual general pattern of a progressive decrease in average size upstream. Seasonal variations are not very pronounced, but there is a tendency for the larvae to be at their maximum size in mid-winter, i.e., at the time when pupae are most abundant.

No correlation between size and abundance or water type could be found by the methods described above.

Simuliidae: Tillyard (1926) states that this family is represented in New Zealand by ten species of the genus *Austrosimulium*, all of which have larvae inhabiting rapid water. As is shown in Table 19, both larvae and pupae are virtually confined to the rapid water of stickles and runs in the Horokiwi.

The local distribution of the Simuliidae is very similar to that of the Chironomidae: they are most abundant in Zone II, rather less so in Zone I, and comparatively scarce in Zones III, IV and V.

The larvae showed no decided seasonal changes in their abundance, but the pupae were much more numerous in October and December, 1940, than at any other time. In the latter month the pupae were two to three times as numerous as the larvae in the collections. No variations, either seasonal or local, were found in the size of the larvae.

Other larvae: This group contains all larvae of this order except the two families dealt with above. It consists of small numbers of a wide variety of forms, none of which is itself sufficiently numerous to be of any significance in the fauna. The group shows no very well-marked local distributions, probably because of its composite nature: it is however apparently scarce in Zone III, and there is a tendency for it to be most abundant in quiet waters. No definite seasonal changes in abundance are apparent.

The group shows clearly the usual decrease in average size upstream but this is probably due largely to variation in the component species in different parts of the stream. There is some indication of a seasonal fluctuation in size with a maximum in April.

Mollusca

Potamopyrgus: Suter (1913) lists six species of this genus as occurring in New Zealand. Of these, at least *P. corolla*, Gould, and *P. antipodum*, Gray, are found in the Horokiwi. Table 19 shows that these forms are very much more abundant in Zone I than in any zones further upstream, and they are also largely concentrated in the pools. There are no definite seasonal changes in their numbers.

The data rather suggest that there may be a seasonal fluctuation in average weight, at least in the lower part of the stream, with the maximum occurring between February and June, but the results are not at all definite. There is however a very definite decrease in size upstream, the average size over the June to December, 1940, period in Zones III to V being less than a quarter of that in Zone I.

No correlation between size and density or water type was found.

Latia: The only species of this genus recorded in New Zealand is *L. neritoides*, Gray. This species is shown by Table 19 to be largely confined to the two lowest Road Branch zones, and is most abundant in Zone III. It was found freely in all types of water, although it was actually most numerous in the samples taken from the two most divergent water types, stickle and pool. It apparently occurred in greatest numbers during the winter and was relatively scarce in middle and late summer.

Its small numbers and limited distribution make it impossible to determine whether there is any local variation in size. There is however an indication that the largest average size occurred in January and February when the numbers were lowest.

ANNELIDA

Oligochaeta: These essentially pool-dwelling animals occurred very much more frequently in Zone I than elsewhere, although they were also fairly abundant in Zone V. They showed no distinct seasonal fluctuations in either numbers or size. Their great diversity of size, due partly to the variety of species concerned, and their relatively small numbers in the middle zones prevented any tests for local size variations from being made.

2. LOCAL EFFECTS.—The results set out in Appendices I and II, and summarized in Table 20, show that during 1940, when stable conditions prevailed, the average fauna in the various parts of the Horokiwi ranged between 236 and 672 animals per square foot, or between 0.181 gm. and 0.914 gm. wet weight per sq. ft. On the basis of weights, the Horokiwi would thus always have a food grade of 3 (i.e., it would be "poor" in food supply) in the scale used by the U.S. Bureau of Fisheries (Davies, 1938). On the other hand, in a similar scale making use of numbers as well as weights (Hazzard, quoted by Hoover, 1937) the average number of animals found per square foot in the Horokiwi would correspond to a food grade of 1 ("exceptionally rich"). Since however the real measure of the amount of food available is provided by weight or volume and not by number of animals, the quantity of bottom fauna present in the Horokiwi must be regarded as poor by North American standards.

TABLE 20. The mean density of the bottom fauna by number (number/square-foot) and weight (mgm./square-foot) for each zone for 1940 and 1941; also the ratio between the two years by number and weight.

Year.		Zone. I.	II.	III.	IV.	V.
1940	Number ..	473·1	384·8	412·8	390·5	446·9
	Weight	647·3	417·4	260·8	235·6	415·2
	Mean weight ..	1·37	1·09	0·79	0·61	0·93
1941	Number ..	238·6	88·1	216·1	170·4	214·0
	Weight	165·6	85·2	97·8	102·9	131·2
	Mean weight ..	0·70	0·97	0·45	0·61	0·61
Ratio	Number ..	0·50	0·23	0·52	0·44	0·48
	Weight	0·26	0·20	0·38	0·44	0·32

Comparison with results obtained from various waters in Great Britain (Pentelow, Butcher and Grindley, 1938, and Allen, 1940, 1941b) suggests that numerically the bottom fauna of the Horokiwi falls, in normal times, within the upper part of the usual range for British streams.

Some quantitative data are also available regarding the density of the bottom fauna in other New Zealand streams. Phillips (1929, 1931) took 41 one-square-foot samples in various rivers in the Wellington district; the numbers of animals recorded in a sample ranged between 18 and 554, with a mean of 196. Percival

(1932) records the results of 14 samples, each of 4 sq. decimetres, taken in various parts of New Zealand; the results are equivalent to densities between 81 and 3,150 animals per sq. ft. with a mean of 1,080. These results are substantially higher than those of Phillips, but this may be partly due to differences in technique. The normal density of the bottom fauna in the Horokiwi is evidently intermediate between the ranges observed by Percival and Phillips in other New Zealand waters and it therefore appears likely that in this respect also the Horokiwi is typical of a large class of New Zealand rivers.

The tables show that while there is on a numerical basis very little difference between the zones in the density of the bottom fauna, well-marked variations in the gravimetric density do occur. Throughout the lower zones there is a progressive decrease upstream in the wet weight of animals found in the average square foot of stream bed; but this tendency is reversed in Zone V, which has a density similar to that of Zone II. We have already seen that almost all the important component groups of the bottom fauna show very similar changes in the individual weights, and this is further illustrated by the average individual weights for all groups given in Table 20. The high values for Zone I are accentuated slightly by the relatively numerous large oligochaetes occurring in this section, but even when these are eliminated the effect is still very definite.

It has been suggested (Phillips, 1931) that the density of the bottom fauna in New Zealand streams is very much greater in places where the forest cover of the banks is undisturbed than it is in cleared country. It is apparent from the above data that this does not apply within the Horokiwi system, where the lowest densities by weight are found in Zones III and IV where the valley is still covered with native bush and with introduced shrubs respectively. Hobbs (1948) has suggested that this belief probably arises from contrasting unstable rivers having open shingle beds with stable streams flowing between bush-clad banks, and concentrating attention on the local vegetation, while ignoring the differences in the stability of the stream bed. The data from the Horokiwi in 1940 show clearly that when stable conditions prevailed in all parts of the stream, the density of the bottom fauna was rather less in the parts of the stream flowing through bush and scrub than it was in open country.

The greatest differences between the fauna of different parts of the stream lie however in its composition rather than in its total density. These differences may be summarized briefly thus:

Zone I is characterized by the presence of relatively large numbers of *Potamopyrgus* and Parnidae, and of moderate numbers of oligochaetes and Chironomidae. Sericostomatid larvae are comparatively scarce. Zone II has a somewhat similar fauna to Zone I, except that the first three of the forms named above are less abundant while the Chironomidae are much more numerous in this zone, particularly in its lower reaches. Sericostomatidae are rather more numerous than in Zone I. The three upper zones are all characterized by the dominance of the four Sericostomatid forms, *Helicopsyche*, *Olinga*, *Pycnocentrodes*, and *"C."* Although *Helicopsyche* is actually the most numerous in all these zones, it is particularly abundant in Zone IV where the other three are somewhat reduced in

numbers. Zone III is also characterized by the presence in limited numbers of Leptoperlidae and *Latia*, both of which are scarce in all other parts of the stream. The fauna of Zone V shows some resemblance to that of Zones I and II in that some of the forms characteristic of these zones, such as Parnidae, *Potamopyrgus* and Oligochaetes are more abundant there than in Zones III and IV. This similarity in the fauna may be associated with the greater resemblance in physical characteristics between the lower zones and Zone V. *Deleatidium* is abundant in all zones. The above characteristic features of the various zones are illustrated by Table 21 which shows the average percentage of each of the major groups in each zone in 1940.

TABLE 21. The mean percentage in the bottom fauna of each of the main groups of animals in each zone in 1940.

	Zone I.	II.	III.	IV.	V.
Sericostomatidæ ..	10·3	36·0	75·8	71·7	65·5
Deleatidium	16·3	13·1	8·9	16·7	17·5
Leptoperlidæ	0·1	0·1	1·7	0·2	0·2
Parnidæ	37·5	9·3	6·5	1·8	7·0
Chironomidæ	16·3	32·6	1·6	4·4	1·9
Potamopyrgus	15·4	2·1	1·7	1·5	2·6
Latia	0·0	0·0	1·2	0·7	0·3
Oligochaeta	1·6	0·3	0·0	0·1	0·4

3. FLOOD EFFECTS.—In the preceding sections discussion has been concentrated on events in 1940 when relatively dry weather prevailed and no significant flooding occurred in the Horokiwi. In 1941 conditions were very different, and a series of major floods occurred with very pronounced effects on the stream. The first of these happened on 12–14th February, and the regular bottom fauna collections were made on 22nd and 24th February, as soon as the water had gone down sufficiently to be workable. The results of this collection show therefore the full effect of this flood upon the fauna. Reference to Appendices I and II shows that the fauna had been very greatly reduced. The effect was most pronounced in Zone II, which has been shown to be the most unstable part of the stream. Here the estimated fauna after the flood was only 14.5 per cent. by number, and 11.7 per cent. by weight, of that estimated to have been present in December. For the other zones substantial, though smaller, decreases were also recorded. The percentages surviving the flood in the other zones were:

Zone I .... 25.5% by number, 23.5% by weight.
Zone III .... 48.3% by number, 27.7% by weight.
Zone IV .... 34.9% by number, 14.9% by weight.
Zone V .... 39.2% by number, 17.5% by weight.

It is clear that in all the zones the flood had destroyed at least half, and generally more, of the bottom fauna, and that the weight of the survivors was proportionately even smaller than their numbers.

The next series of bottom fauna collections was taken on April 9th, 10th and 21st. As Table 15 shows, only one slight flood occurred between these two series of collections, and a considerable degree of recovery of the fauna had taken place. The estimated fauna for Zone II had risen to 38.4 per cent. by number and 31.7 per cent. by weight of the December, 1940, level, and the corresponding figures for the other zones were:

Zone I .... 68.4% by number, 75.8% by weight.
Zone III .... 109.5% by number, 48.3% by weight.
Zone IV .... 75.7% by number, 68.3% by weight.
Zone V .... 90.6% by number, 29.4% by weight.

From July onwards a succession of floods and periods of high level kept the Horokiwi in a disturbed state, and these culminated in the severe flood of 2nd October. The final series of bottom fauna samples was taken not long after this, on 20th October. As already explained, this was only a partial series, and the results are therefore somewhat less reliable than those based on the earlier series. It is apparent however that this flood had reduced the fauna to a level which was very much below that prevailing in April, 1941, and numerically even below that existing immediately after the flood in February, 1941.

These results show that after January, 1941, the succession of floods reduced the bottom fauna of the Horokiwi to a very much lower level than that of 1940, and kept it at the new low level. There was possibly a period in May and June when it built up again to the normal density, but this would be only a passing phase, which was destroyed by the action of further floods. It is probable that the average density of the fauna for the year as a whole was between 40 per cent. and 50 per cent. of that of 1940 in most parts of the stream, and as low as 20 per cent. to 25 per cent. in Zone II. It is noteworthy that this zone, which on purely physical grounds was described earlier as being in an unstable state, suffered a much more pronounced reduction in its bottom fauna than any of the other zones.

The reduction in the weight of the fauna by the February flood was even greater than the reduction in the number of animals. This was probably caused by a decrease in the average size of many species of insect larvae due to the normal replacement between December and February of mature larvae of one generation by young larvae of the next. It is noteworthy that the average size of all groups in February, 1941, is much less below that obtained in the December, 1939–January, 1940, series than it is below that recorded in December only in 1940.

TABLE 22. The ratio between the mean density in February 1941 and the combined mean for April and December 1940 for a number of bottom fauna animals.

Hydropsyche	0·84	Leptoperlidæ	0·29
Rhyacophilidæ larvæ ..	0·25	Parnidae imagines	0·20
Helicopsyche	0·51	,, larvæ	0·19
Olinga	0·37	Chironomidæ larvæ	0·06
Sericostomatidæ Type "C" larvæ	1·05	Simuliidæ larvæ	0·05
Pycnocentrodes larvæ	0·09	*Potamopyrgus*	0·10
Coloburiscus	0·07	Oligochaeta	0·21
Deleatidium	0·21		

The extent of the damage by floods varied considerably between the different forms in the bottom fauna. Table 22 shows the mean density of each group in the February, 1941, collections expressed as a proportion of its mean for the April, 1940, and December, 1940, values, since this should give an indication of the probable February values under normal conditions. No data are given for pupae or for forms which show a wide divergence between December and April values, since in these cases the estimates of normal February densities would be unreliable. The rapid-water forms appear in most cases to be less subject to flood damage than the quiet-water species. Thus, the two forms which suffered strikingly little from the floods, *Hydropsyche* and Sericostomatid "C." are both inhabitants of rapid water. At the other extreme, the three outstandingly quiet-water animals, *Potamopyrgus*, Parnidae larvae and oligochaetes, were all very seriously reduced in numbers. The principal exceptions to this general rule are provided by the three rapid-water groups, Leptoperlidae, Simuliidae and *Coloburiscus*. The exceptional damage suffered by the Simuliidae may be partly because they are normally most abundant in Zone II which was the zone most severely disturbed by the flood. The heavy damage suffered by the Chironomidae was also probably due to this cause.

2. NATIVE FISH

(a) Nature of Observations

The techniques used for taking fish in this investigation were designed essentially for taking trout, and were therefore less suitable for taking other species of fish with different habits. These methods will be discussed in detail in a later section, but they consisted mainly of a variety of seining techniques, and of the use of handnets in conjunction with powerful electric torches at night. These methods were very effective in taking fish which normally swim clear of the bottom, but took relatively few of the species which lie on the bottom among the stones, or which seek the deepest and most inaccessible covers when disturbed. Consequently some of the native species, such as *Retropinna osmeroides* and *Galaxias attenuatus*, were taken freely, but relatively small numbers of other species, such as *Gobiomorphus* spp., *Anguilla* spp. and *Galaxias fasciatus*, were caught. Owing to the limited time available, the observations made on the native fish which were taken in the nets were much less complete than the observations on the trout. They were generally confined to the recording of approximate numbers of each species taken in each section, and a few specimens were occasionally preserved for the examination of stomach contents. The data available regarding the native fish fauna therefore deal mainly with the distribution and approximate abundance of each species, and include some general observations regarding their food.

(b) Results

The data available for each genus are discussed in the following sections.

1. Anguilla.—Two species of fresh-water eel are known from New Zealand and both are present in the Horokiwi. These species have been shown by Griffin (1936) to be the Long-finned eel, *Anguilla dieffenbachii*, Gray, and the Short-finned eel, *A. australis schmidtii*, Phillipps. The distribution of these two species in New

Zealand has been discussed by Cairns (1942), who concludes that generally the females of *A. dieffenbachii* penetrate well inland, while those of *A. australis schmidtii* are rarely found outside coastal waters except in lakes and warm, sluggish rivers. The males of both forms appear to resemble other species of the genus by being largely confined to tidal waters. Cairns quotes the results of some collections made in the Horokiwi, in which 123 eels, taken "upstream," were all *A. dieffenbachii*, while 27 eels taken in the "estuary" included 21 *A. australis schmidtii* and 6 *A. dieffenbachii*; all were females. Although the actual site of the collections was not precisely described, these results suggest that the normal conditions described above prevail in the Horokiwi.

Approximately 435 eels were handled during the investigation and nearly 300 others were observed in the water at night. Among these only three were recorded as being *A. australis schmidtii*, and it is unlikely that many other individuals of this species escaped notice, particularly among those handled. Relatively few collections by methods which would have taken eels were made in the tidal reaches of the stream, i.e., in the area normally inhabited by this species, and its absence from collections is therefore not unexpected. Two of the specimens recorded were taken in Section M 8, which is well within tidal influences; the other was taken in Section M 108, at a distance of about 2,000 yards above the mouth.

It is apparent therefore that the only species which is found in the same parts of the stream as the trout in sufficient numbers to be of any significance is *A. dieffenbachii*. This was found commonly in all parts of the stream, and appeared to show no localized distribution, except that brought about by its need for deep and efficient cover. In the lower reaches (Zones I and II) this cover was generally formed by undermined sods along the banks, and occasionally by old tree roots and accumulations of brushwood. In the upper reaches the main forms of good eel cover were brushwood, crevices in rocks and bank protection structures, and under boulders, and, more rarely, fallen sods. Over the whole stream the number of eels recorded was approximately one-third of the number of trout observed or taken in the same work, and this ratio also applied in most of the separate zones. The biggest variations were in Zone III, where eels were relatively numerous, and in Zone IV, where they were relatively scarce. The actual and relative numbers of eels and trout recorded from each zone in each two-month period are shown in Table 23. It is evident from the table that during the winter periods, May–June and July–August, the relative numbers of eels recorded were very much lower than at other seasons. This is probably because this species, like most freshwater eels of temperate regions, hibernates to some extent during the cold weather. Even fewer eels would probably have been recorded during the winter months if the usual netting techniques had not involved thorough exploration or disturbance of all accessible covers so that hibernating eels were likely to be disturbed.

Cairns has shown that *A. dieffenbachii*, when less than about 75 cm. in length, feeds mainly on the invertebrates of the bottom fauna, and takes a high proportion of Trichoptera and Ephemeroptera. It will be shown in a later section that these groups form a large part of the food of trout in the Horokiwi, and it would therefore appear that some degree of competition for food between the two species of

TABLE 23. The actual and relative numbers of trout, eels and bullies recorded from each zone in each two-month period.

Zone.	Jan.–Feb.	Mar.–April.	May–June.	July–Aug.	Sept.–Oct.	Nov.–Dec.	Total.
I—Trout	41	123	184	37	20	81	486
Eels	21	52	23	15	0	49	160
Ratio E. : Tr.	*0·51*	*0·42*	*0·12*	*0·41*	*0·00*	*0·61*	*0·33*
Bullies ..	165	473	305	71	179	300	1493
Ratio B. : Tr.	*4·03*	*3·85*	*1·65*	*1·92*	*8·95*	*3·71*	*3·08*
II M—Trout ..	44	31	403	106	74	82	740
Eels ..	15	41	49	15	45	54	219
Ratio E. : Tr.	*0·34*	*1·32*	*0·12*	*0·14*	*0·61*	*0·66*	*0·30*
Bullies ..	31	0	174	11	19	75	310
Ratio B. : Tr.	*0·71*	*0·00*	*0·43*	*0·10*	*0·26*	*0·92*	*0·42*
II R—Trout ..	0	0	90	0	7	0	97
Eels ..	0	0	40	0	5	0	45
Ratio E. : Tr.	..	..	*0·44*	..	*0·71*	..	*0·46*
Bullies ..	0	0	63	0	2	0	65
Ratio B. : Tr.	..	..	*0·70*	..	*0·29*	..	*0·67*
III—Trout	12	19	102	10	15	36	194
Eels	7	13	52	3	29	17	121
Ratio E. : Tr.	*0·58*	*0·68*	*0·51*	*0·30*	*1·93*	*0·47*	*0·62*
Bullies ..	15	7	53	8	30	0	113
Ratio B. : Tr.	*1·25*	*0·37*	*0·52*	*0·80*	*2·00*	*0·00*	*0·58*
IV—Trout	79	84	64	34	69	160	490
Eels	30	13	8	3	10	29	93
Ratio E. : Tr.	*0·38*	*0·15*	*0·12*	*0·09*	*0·14*	*0·18*	*0·19*
Bullies ..	1	2	1	0	1	0	5
Ratio B. : Tr.	*0·01*	*0·02*	*0·02*	*0·00*	*0·01*	*0·00*	*0·01*
V—Trout	23	40	73	18	43	26	223
Eels	19	26	16	2	15	2	80
Ratio E. : Tr.	*0·83*	*0·65*	*0·22*	*0·11*	*0·35*	*0·08*	*0·36*
Bullies ..	0	1	1	1	0	0	3
Ratio B. : Tr.	*0·00*	*0·02*	*0·01*	*0·06*	*0·00*	*0·00*	*0·01*
Total—Trout ..	199	297	916	205	228	385	2230
Eels ..	92	145	188	38	104	151	718
Ratio E. : Tr.	*0·46*	*0·49*	*0·21*	*0·19*	*0·46*	*0·39*	*0·32*
Bullies ..	212	483	597	91	231	375	1989
Ratio B. : Tr.	*1·06*	*1·63*	*0·65*	*0·44*	*1·01*	*0·98*	*0·89*

fish must occur. Cairns has also shown that eels more than 75 cm. in length feed to a considerable extent upon small fish and that in some waters these may include many trout.

Since in all parts of the Horokiwi the numbers of eels are comparable with those of the trout, the quantity of invertebrates which they consume is probably significant in relation to that eaten by the trout. The quantity of young trout which they eat is probably also appreciable. Much more precise data are however required regarding both the size and composition of the eel population, and the quantity of food consumed by individual eels, before the true significance of either the competition for food, or the predation, can be determined.

2. GALAXIAS.—Three species of this genus have been recorded from the Horokiwi: *G. attenuatus* (Jenyns), *G. fasciatus*, Gray, and *G. robinsonii*, Clarke (= ? *G. brevipinnis*, Guenther). Of these the most abundant is *G. attenuatus*; this is a migratory species, which forms the basis of the New Zealand "whitebait"

industry. The adults spawn in tidal marshes at the height of the autumnal spring tides; the eggs hatch when they are next covered by a spring tide, two or four weeks later; the young larvae are carried out to sea and ultimately return in the late larval "whitebait" stage; they ascend the rivers and there become pigmented and metamorphose into the adult stage, known as the inanga; the adults finally descend to the tidal marshes to spawn (N.Z. Marine Dept., 1930, 1931, 1932).

In the Horokiwi the ascent from the sea takes place about September and October, and the species is abundant in the lower reaches during the next few months. It does not, however, appear to penetrate further upstream than the junction of the Road and Back Branches. After February it rapidly becomes less abundant, and by mid-winter has become so scarce that no specimens were ever recorded during the months of July and August. A few individuals appear to survive the winter, however, since occasional very large specimens were taken in September and October.

It appears that this species only occurs in sufficient numbers to give it any significance in relation to the trout in the lower part of the Main Water, and for a period of seven months, i.e., October to April. The principal relationships which seem likely to occur between this species and the trout are competition for food and predation by the trout on *G. attenuatus*. Only 14 stomachs of this species have been examined from the Horokiwi, with the results shown in Table 24. The amount of data is much too small to permit of any quantitative conclusions being drawn, but the majority of the forms found in the few stomachs examined are also eaten freely by trout at some period in their life, although a few, such as Parnidae larvae and ostracods, are rarely taken by trout. It appears therefore that there is a substantial overlap between the food of *G. attenuatus* and of trout, which must lead to some degree of inter-specific competition.

More data are available regarding the extent to which the trout prey upon *G. attenuatus*. Outside the months October to April trout are not likely to have access to this fish, while trout in their first year are normally too small to eat other fish. If these groups are eliminated, 53 trout remain which might have consumed *G. attenuatus*. In fact, however, not a single one of these contained this species; it appears therefore that *G. attenuatus* is not of any great significance as a source of food for trout in the Horokiwi, although it is of course probable that it is sometimes eaten.

Galaxias fasciatus, the kokopu, is not known to be migratory, and is typically found in stable streams which possess good pools or abundant shelter and are more or less completely overhung by trees, and particularly by undisturbed native bush. It appears to have found a secondary habitat in very small streams flowing through grassland, which are deeply entrenched and have relatively good pools; in these its shade requirements are probably provided by long grass overhanging and often almost completely hiding the streams.

In the Horokiwi its distribution is fully in accord with the typical conditions. Only a single specimen was seen in the open waters of the Main Water, while it was never recorded from the lower open part of the Road Branch. It was however regularly present where the stream flows through the native bush in the lower part of Zone III, and occasional specimens were taken or observed in areas where

the stream was largely overgrown by gorse bushes in the middle part of Zone III and in Zone IV. In the open waters of Zone V the only specimen recorded was taken in the pool which forms the upstream limit of the observed area. This pool is fed by a small tributary which flows through a narrow bush-clad valley, and which contains numerous kokopu. The only other part of the Horokiwi system in which this species was recorded was a small grass-grown stream of the type described earlier, which joined the Horokiwi from the east about 4,000 ft. from the mouth.

The only part of the observed area in which *G. fasciatus* was at all numerous was therefore the lower bush-covered part of Zone III. That it was relatively uncommon even here is shown by the fact that some very thorough netting carried out in this region in May and June, 1941, yielded 38 trout, but only 15 kokopu. Since, as will be shown later, trout are less numerous in this area than in any other part of the Horokiwi, it seems unlikely that the kokopu is sufficiently abundant anywhere in the system to have any influence on the trout population.

Galaxias robinsonii is a relatively rare species, and virtually nothing is known of its distribution or habits in any part of New Zealand. Its presence in the Horokiwi system is only known from two specimens which were netted in December, 1939, from a small pool about half a mile above the upper limit of the observed area. It is not therefore known to occur at all in this region.

TABLE 24. Results of the examination of the stomach contents of small samples of native fish from the Horokiwi.

	Species of Fish.			
	Galaxias attenuatus.	*Gobiomorphus* spp.	*Retropinna osmeroides.*	*Agnostomus forsteri.*
Number examined	14	14	8	12
Average number of animals in stomach	22·7	8·4	16·7	143·1
Percentage composition—				
Deleatidium nymphs	13·5	25·4	18·7	2·4
Sericostomatidæ larvæ	1·9	0·8	6·7	25·7
Hydroptilidæ larvæ	4·4	0	0	0
Other Trichoptera larvæ ..	3·1	9·3	3·0	0·1
Parnidæ larvæ and imagines ..	6·0	3·4	7·5	20·6
Chironomidæ larvæ and pupæ ..	26·7	44·8	33·6	1·7
Other Diptera larvæ and pupæ ..	12·6	0	1·5	0·2
Other insect larvæ	0	0	0·7	0·1
Other insect imagines	4·4	0	20·8	0
Crustacea	3·8	0·8	1·5	0·4
Hydracarina	0	0	0	0·1
Potamopyrgus	22·6	15·3	0·7	45·4
Oligochaeta	0·9	0	5·2	3·3
Total	99·9	99·8	99·9	100·0

3. GOBIOMORPHUS.—Stokell (1941a) has recognized three species of this genus, commonly known as "bullies," as occurring in New Zealand. Two of these, *G. radiata* (Cuv. and Val.) and *G. basalis* (Gray), have been identified from the Horokiwi,

PLATE VII (a). A typical stickle showing the shallow rippling water; such conditions are very abundant in Zone II M where this photograph was taken.

PLATE VII (b). A run, also in Zone II M; in this water type the flow is rapid but the stream is confined in a narrow channel and is relatively deep; the flow is turbulent rather than rippled.

PLATE VII (c). A flat in Zone IV; the shallow quietly-flowing water which is the distinctive feature of this water type allows the stones of the streambed to be clearly visible.

PLATE VIII (a). A typical pool in Zone I; throughout most of Zones I and II pools are generally formed on a bend where the stream is eating into the bank. On the outer side of the bend there is frequently a high bank of clay which drops almost vertically into deep water; on the inner side, the bank is usually low and grades gently into the water.

PLATE VIII (b). In Zones III, IV and V, where the flood-plain is relatively very small, pools are commonly formed where the stream impinges against a rocky part of the valley wall. Frequently, as in this typical example in Zone III, a nose of rock projects into the pool.

but they were not normally distinguished in the field, and in the following discussion they have been grouped together. The numbers of *Gobiomorphus* and of trout recorded from each zone are compared in Table 23. For reasons discussed earlier the bullies were collected very much less efficiently than were the trout; the relative efficiency would however be more or less the same in all zones, and the data should therefore give an approximate indication of the relative abundance of bullies in the different zones. Three regions can be distinguished in relation to the distribution of these fish; in the lowest region, consisting of Zone I, they are very abundant; in the middle region, consisting of Zones II and III, they occur frequently but are not abundant; and in the uppermost region, which consists of Zones IV and V, they are scarce. In general the numbers of *Gobiomorphus* appear to decrease steadily upstream. Insufficient is known of the biology of any species of this genus to provide any explanation of this phenomenon; but that it is not a simple effect of altitude is indicated by the fact that a species of *Gobiomorphus* was found to be common above the observed area in the tributary stream already mentioned as containing abundant *G. fasciatus*. Such specific identifications as were made in the field suggested that *G. basalis* is the more frequent form in the lower reaches, but that it tends to be replaced further upstream by *G. radiata*.

The most probable relationships between trout and *Gobiomorphus* are those of competition for food, and of predation by the trout on *Gobiomorphus*, although Hobbs (1940) has also recorded predation by bullies upon trout fry. Table 24 summarizes the results of the examination of the stomach contents of a small sample of 14 bullies, all taken in the lower part of Zone I, where they are most abundant. From this sample it appears that the food of *Gobiomorphus* is not dissimilar from that of small trout, particularly in the high proportion of *Deleatidium* nymphs and chironomid larvae which it contains. This being so, there may be some degree of competition for food between the two forms, particularly in Zone I where *Gobiomorphus* is most abundant. Trout of less than a certain size do not often eat other small fish, and in fact no fish were found in the stomachs of trout much before the end of their second year. The stomachs of 91 trout of this age or older were examined, and only one was found to contain *Gobiomorphus*, and this only a single specimen. It would appear therefore that in the Horokiwi bullies are not very frequently consumed even by those trout which are large enough to take them.

4. Retropinna.—Five species of this genus, the smelts, have been recognized by Stokell (1941b and 1943) in New Zealand. Only one of these, *R. osmeroides*, Hector, has been found in the Horokiwi. This is a migratory species and appears to be generally similar in its movements to *Galaxias attenuatus*, although its spawning habits have not yet been observed. It appears to enter the Horokiwi slightly later than *G. attenuatus*, and has not been recorded in large numbers earlier than the latter part of November. Correspondingly it continues to be abundant to a later date than the inanga, and is still plentiful as late as May. It also penetrates much further up river than the inanga, and a single specimen was recorded on 9th April, 1941, as far upstream as Section R 527, in the middle of Zone IV. It does not however often occur above Zone III where it is regularly found during the late summer and autumn in small numbers, and it is abundant only in Zones I and II.

Only eight stomach contents of this species have been examined from the Horokiwi, and the results are given in Table 24. This small sample suggests that the food of this fish may be similar to that of young trout. In this case there may possibly be some degree of competition for food between these species in the regions where *R. osmeroides* is most abundant, i.e., in Zones I and II. Only one of the 91 trout already referred to as being old enough to eat small fish contained *Retropinna* and this contained two specimens. Some of these trout were taken from waters beyond the area normally occupied by *Retropinna*, or at seasons when this fish is scarce or absent from the Horokiwi. Despite this it seems unlikely that *Retropinna* is eaten at all frequently by trout in the Horokiwi.

5. Agnostomus.—The species of native fish already discussed are either truly fresh-water forms or migratory ones which are restricted to fresh or estuarine conditions for a part of their life-cycle. There are in addition two marine species which enter the river and therefore overlap with the trout to some extent in their environments. The first of these is *Agnostomus forsteri* (Cuv. and Val.), the yellow-eyed mullet, or herring; this is a marine fish which sometimes enters fresh water, and may travel a short distance above the influence of the tide. In the Horokiwi this species, which usually occurs in shoals, has been recorded from as far up the river as section M 22, which is about 1,800 ft. from the mouth of the stream, and about 1,000 ft. above the limit of tidal influence. It is however most common in tidal waters and shoals of several hundreds were frequently seen in the lowest reaches. The results of the examination of the stomach contents of 12 fish are given in Table 24. Some of the stomachs contained appreciable quantities of diatomaceous ooze in addition to the animals listed in the table. The table shows that the food of this species differs strikingly from that of the other native fish, most of which were taken at the same point on the river and at the same time. In this sample the greater part of the food consisted of Sericostomatid larvae, Parnidae larvae and imagines, and *Potamopyrgus*. All of these, except the Parnidae larvae, are freely eaten by the larger trout, and the large shoals and relatively large individual size of these fish may therefore cause quite significant competition with trout in the short length of the stream which they frequent.

The comparatively large size of this fish probably tends to make it little subject to predation by trout.

6. Tripterigion.—The remaining marine species which enters the Horokiwi for a short distance is a blenny of the genus *Tripterigion*. This species appears to be the same as *T. robustum* described by Clarke (1879) which Phillipps (1921) has identified with *T. varium*, Forster. This species is found only in the estuarine reaches of the Horokiwi and probably only in waters where there is always some degree of salinity. It has not been recorded farther upstream than section M 5. Owing to the short length of the river which it inhabits it is unlikely to have any significant relationship with the trout population.

7. Geotria.—In addition to the true fishes referred to above, the lamprey, *G. australis*, Gray, is also present in the Horokiwi. The larval stages are not uncommon in suitable mud in backwaters in the lower part of the stream, and a few adults have also been observed. In view of its burrowing habits it seems

unlikely that this animal has any significant relationship to the trout either as a competitor for food or as prey or predator.

It seems therefore that, except for the eels, the native fish fauna of the Horokiwi decreases rapidly upstream in numbers of both species and individuals, and that these fish are probably insufficiently numerous above Zone I, or possibly Zone II M, to have any significant effect on the trout population, either as competitors for food, or as a source of food themselves.

3. AQUATIC BIRDS

A number of birds which feed partly or entirely on fish were observed on the Horokiwi on several occasions.

The Black Shag (*Phalacrocorax carbo*) was frequently seen passing along the valley, apparently between feeding-ground on the Pahautanui Inlet and roosting places in the bush to the north-east of the Back Branch. These birds were, however, very rarely seen to stop and fish in the Horokiwi.

The Whitefronted and Caspian Terns (*Sterna striata* and *Hydroprogne caspia*) were sometimes seen fishing the lower waters of the Horokiwi, but it was never possible to see what species of fish they caught.

The Kingfisher (*Halcyon sanctus*) was seen from time to time in all parts of the valley.

The Bittern (*Botaurus poiciloptilus*) occurred occasionally in the swampy ground adjoining the stream in the lower part of Zone I, but was never seen on the stream itself.

General observations suggested that it was unlikely that any of these birds were significant predators on the trout in the Horokiwi, although the two species of terns probably took more fish than the other species.

4. SUMMARY

Estimates of the total bottom fauna were based on the results of series of one square-foot samples taken generally at two-monthly intervals. The series usually consisted of 20 samples, and was taken from each water type in each zone.

From the samples and the results of the physical survey estimates have been made of the mean density and composition of the bottom fauna by number and weight in each zone at each sampling date. These estimates are presented in Appendices I and II.

The bottom fauna normally contains 300–600 animals to the square-foot, with a wet weight of 0.2 gm. to 0.9 gm. The reliability of the estimates appears to be about ± 50 per cent. for 95 per cent. confidence.

The distribution of the various animals in the fauna is discussed and it is shown that many of the forms are characteristic of particular parts of the stream or of particular water types. The lower zones are characterized by the presence of *Potamopyrgus*, Parnidae and oligochaetes, while the upper zones are characterized by the abundance of four species of Sericostomatidae. Zone II is particularly rich in Chironomidae and Simuliidae, and Zone III is the only one containing Leptoperlidae and *Latia* in any numbers.

The average size of many species shows a definite tendency to decrease progressively upstream, although in several instances this trend is reversed at the top of the stream and the average size is greater in Zone V than in Zone IV. As a result the density by weight of the bottom fauna also decreases upstream except for a final increase in Zone V, despite the fact that there is very little difference between the numerical density of the faunas of the various zones.

The severe flood of February, 1941, caused great destruction of the bottom fauna; there was a considerable amount of recovery in the next few months but from July onwards the succession of floods caused further damage. The destruction was particularly severe in the unstable conditions of Zone II. It is probable that as a result of the floods the average density of the fauna in 1941 was only 40–50 per cent. of that in 1940, while in Zone II it may have been as low as 20–25 per cent.

The collecting methods used were less effective for taking some of the bottom-living native fish than for taking trout. Nevertheless they provide an indication of the distribution of the various species, and a rough measure of their abundance in relation to trout.

The largest and most widely distributed of the native fish is the eel; outside the tidal waters only the females of *A. dieffenbachii* were abundant. These were common in all parts of the stream and appeared to be about one-third as numerous as the trout. It is likely that they have a significant relationship with the trout, both as competitors for food and as predators.

The only other native fish of any importance are the inanga, *Galaxias attenuatus*, the smelt, *Retropinna osmeroides*, and two species of bullies, *Gobiomorphus*. These are all most abundant in Zone I and become rapidly less numerous further upstream; *Gobiomorphus* is found in small numbers in all parts of the stream, but *R. osmeroides* is rarely found above Zone III and *G. attenuatus* is restricted to Zones I and II. All these species compete to some extent with the trout for food and are also probably sometimes eaten by large trout. It is unlikely however that they have any significant effect on the trout population except perhaps in Zone I.

PART IV

The Trout Population

1. OBJECTS

The fundamental object of the whole of the present investigation was to study the factors affecting the production of trout in a typical stream. In particular it was intended to examine the relationships between the trout production, the quantity of food available and consumed, and the quantity of trout taken by anglers, i.e., the crop. The physical background in which the trout were living, and the density and composition of the bottom fauna which forms the main source of food, have been dealt with in the preceding sections. The studies of the trout themselves had to yield data regarding the quantity of trout produced, the quantity and composition of the food actually eaten, and the quantity and nature of the fish taken by anglers.

Measurement of the production of trout involved the determination, at frequent intervals, of the number and size of the survivors of each year-class. It was therefore necessary to make regular estimates of the size and composition of the trout population, and to study the rate of growth of each year-class. Since well-marked differences occurred between different sections of the stream, it was essential to make independent studies for each of the principal regions. These regions were the zones referred to in the preceding sections of this paper, and the basis for the selection of these particular regions will be discussed in the sections dealing with the growth of the trout.

In the same way, study of the quantity and composition of the food consumed by the trout required knowledge of the food being eaten by each year-class throughout the year. This could most simply be obtained by the examination of the stomach contents of adequate samples of fish, taken in all the zones at regular and relatively short intervals. For the study of the angling catch it was necessary to obtain reasonably complete records of the numbers and sizes of the fish taken by anglers in each season. The data should also, as far as possible, enable separate estimates to be made of the catch in each zone, and should show the distribution of the catch throughout the season.

2. SCHEME OF WORK

The study of the trout population, like that of the bottom fauna, had to be based on the investigation of sample regions. It was found that, as with bottom fauna, it was only possible to conduct regular observations on six of the ten stations originally planned, and the same six stations were used. Each of these was regularly netted as thoroughly as possible at three-monthly intervals. In addition to forming a basis for estimation of the size and composition of the population, the fish taken also provided material for study of the growth rates of each year-class, and for

examination of the food being consumed by the fish. In order to give more continuous data regarding food and growth, additional material was obtained from each station once a month. On these occasions the amount of netting was limited to that necessary to provide adequate material for the food and growth studies.

To provide more complete data on local growth effects and the distribution of the population along the course of the stream, special netting programmes were carried out in the autumn of each year. In 1940 these were restricted by weather and inadequacy of technique, and work was largely confined to Zones I and II. By 1941 more efficient netting methods had been worked out, and more favourable weather prevailed. The proportion of the stream netted was approximately half. The method adopted was to divide the stream into a series of sections of approximately equal length and to net the alternate ones as thoroughly as possible. In the Main Water the length of these sections was generally between 850 ft. and 1,000 ft., and in the Road Branch between 1,350 ft. and 1,450 ft.

To test the efficiency of netting, and to study movements and rate of growth, all fish which were of sufficient size were marked prior to release, unless they had to be killed for the examination of stomach contents. For a few months after hatching the young fry were collected at intervals of less than a month on account of the relatively rapid changes which take place at this time. In the 1939–40 season this was done irregularly, and the samples were not concentrated at fixed stations although they were most frequently taken in Zones I and IV. In 1940–41 however collections were taken more regularly, and as far as possible they included all the stations under routine observation.

To obtain data regarding the number and distribution of mature fish, and to enable estimates to be made of egg and fry production, the stream was patrolled regularly during the spawning season, and the position and subsequent history of all redds found were recorded. In 1939 the work was largely experimental, and the record obtained was probably very incomplete. In 1940 the technique was improved and good weather conditions prevailed throughout the spawning season, so that a reasonably complete record of the visible redds was obtained. In 1941 the spawning season was very seriously interfered with by floods, which made the identification of redds difficult on account of the frequent disturbances of the shingle. Only an approximate record of the number of redds was therefore obtained in that year. Some data regarding the number of eggs deposited and the extent of mortality in the redds were obtained in 1940 and 1941 by digging out the contents of a small series of sample redds.

The angling catch was studied by means of a diary scheme. An effort was made to contact personally as many as possible of the anglers fishing the Horokiwi, and to persuade them to keep a record of their catches on a special diary form, and to send it in at the end of the season.

3. METHODS

The collection of trout for the various purposes of this investigation was mainly done by netting. In the quarterly routine nettings and in the annual, more complete, nettings, considerable care was taken to work as effectively as possible, as one of the main objects was to obtain an estimate of the density of the population.

The nets used were of ½-inch stretched mesh of 32/9 cotton twine. They were mounted on a head-rope of 1-inch circumference hemp rope with 3-inch diameter corks at 18-inch intervals. The foot of the net was mounted on iron chain weighing 4 oz. per foot; this was found to lie more closely to the bottom than a rope with leads at intervals, particularly in rapid water, and was therefore more effective for taking bottom-living fish and small trout. The nets were generally 4½ ft. deep, and a series ranging in length from 4 ft. to 26 ft. was used as circumstances required. These nets were constructed so that they could be linked together to form longer nets when necessary. At first a poke net 12 ft. long, and with a mouth 4 ft. wide, as described elsewhere (Allen, 1941b) was used with the plain seine nets linked to it to form wings. It was however gradually abandoned as it was found unsuitable for use in the Horokiwi. The general procedure adopted was to work upstream through the station being netted; a stop-net was set across the bottom of the station and then a convenient length of water above it, usually 20 to 40 yards, was netted. The methods used depended largely on the type of water; shallow rapid water was seined straight down to the stop-net, and the seine was either swung to one side and beached, or else taken straight down to the stop-net which was then lifted quickly; deeper and quieter water was generally seined upstream to a suitable natural break; deep pools with one sheer bank were seined by laying the net along the sheer bank and drawing straight across. When the open water had been cleared of fish, all suitable covers were netted individually. This was done with a special net about 11 ft. long, and 3 ft. deep, with handle tabs at the ends of the head and foot lines. This was laid round the cover, and while one operator held the downstream end close to the bank, the other operator started at the upstream end and worked downstream, driving the fish ahead of him until the operators met and the fish were contained in a bag of netting which was then lifted out. This method proved particularly suitable for a stream like the Horokiwi where much of the cover was formed by fallen sods along the banks, and a high proportion of the fish caught in shallow water was taken in this way. These various procedures were repeated until no more fish could be caught, and then the stop-net was moved up to the foot of the next part of the station, and the process was repeated. When the head of the station was being approached, a second stop-net was set across the stream there when necessary to prevent any fish being driven out of the station.

In addition to the methods described above, netting was also done at night. In this method the water was searched with powerful electric torches, and the individual fish were collected either with a hand-net or with a short seine mounted between long poles while dazzled by the light. This method was used for two special purposes; fry in their first few months of life, while they were still small enough to lie between the stones and allow an ordinary seine to pass over them, could be easily taken in this way; it was also used to take fish of all ages at night in order to compare their stomach contents with those of fish taken during daylight. The fish caught, by whatever method, were either killed immediately if they were required for stomach contents, or placed in a live-box in the stream until they could conveniently be weighed, measured, and, if necessary, tagged. The fish kept for stomach contents were normally weighed and measured while still fresh by the same methods as were used for the live fish; before May, 1940, the fish

of the 1939 year-class were only weighed after they had been preserved for some time in 4 per cent. formalin at the laboratory.

All fish were measured to the fork of the tail on a measuring board of conventional design, measurements being made to the nearest millimetre. Weighings were made on a spring balance, a series of different ranges being used for fish of different sizes. Weights were read to the nearest 1 gm. for fish up to 100 gm., the nearest 5 gm. for fish up to 500 gm., and to the nearest 10 gm. for larger fish. Fish smaller than about 5 gm. were weighed in batches, and their individual weights were afterwards approximately determined if necessary by apportioning them in proportion to the cube of their lengths. From all fish more than a few months old scale samples were taken from between the back and the lateral line just in front of the dorsal fin, and were preserved in envelopes on which the particulars of the fish were written. Some of the scales in each sample were ultimately mounted in glycerine jelly for reading with a projector.

Fish were tagged by attaching a small oxidized silver disc to the dorsal fin; this disc was 4.7 mm. in diameter and weighed 0.025 gm. It carried two or three letters and numbers and was pierced by a small hole, by which it was threaded on to a piece of silver wire 0.3 mm. in diameter. The wire was passed through the base of the dorsal fin behind the second large ray and then fastened in a loop round the front of the fin. It was adjusted so that the tag lay as closely against the fish as possible. This type of tag, which was designed to be as light as possible and unlikely to catch seriously in covers, proved to be satisfactory for use on fish about 15 cm. in length or more.

The observations on redds were made by examining carefully either the whole stream or selected lengths of it, and recording all redds seen. The record included the size, position and apparent freshness of each redd. Redds were classified roughly into five categories according to the width of the excavation, using the following scale:

Very small redds	less than 1 ft. wide.
Small redds	1 ft. to $1\frac{1}{2}$ ft. wide.
Medium redds	$1\frac{1}{2}$ ft. to $2\frac{1}{2}$ ft. wide.
Large redds	$2\frac{1}{2}$ ft. to $3\frac{1}{2}$ ft. wide.
Very large redds	over $3\frac{1}{2}$ ft. wide.

Where spawning fish had disturbed the gravel, but separate redds could not be distinguished, "disturbed areas" were recorded, and their approximate dimensions noted. Where a redd had been begun, but had either been abandoned or was still very unfinished when found, it was entered as a "trial scrape." The position of each redd was identified by recording the number of the section in which it was situated, the distance up or downstream from a convenient landmark, and the distance from either the right or left bank.

The apparent freshness of a redd was determined by the ease with which it could be seen, and depended largely on the contrast between the disturbed stones and the undisturbed stream bed, and upon the clearness of the mound and pit formation. In settled weather fresh redds were very clearly visible on account of the heavy diatom growth on the undisturbed stones, which contrasted sharply with the clean

stones of the redd. Under these conditions a redd became gradually less distinct as its stones became covered with diatoms. Even small floods tended to wash all the stones comparatively clean, with the result that even fresh redds were harder to see, while subsequent floods would quickly blur the outlines of a redd. The redd count was less reliable therefore during unsettled weather. Redds which were clearly visible were classified as "fresh"; they became "obscure" when they were difficult to see, and particularly when it was considered that they would have been overlooked if they had not previously been recorded; and they "disappeared" when they could no longer be distinguished even when their position was known.

Patrols for the purpose of counting the redds were made at intervals of a week or ten days during the height of the spawning season if weather permitted, and unless floods had intervened it was generally possible to determine with reasonable certainty whether a redd previously logged had been disturbed by subsequent spawning. During the settled weather of 1940 it was generally found that most redds progressed to the "obscure" stage in two to three weeks, and "disappeared" in about three to five weeks after they were first observed. There was however a good deal of individual variation whch depended upon the size and position of the redd.

The contents of the redds were investigated by digging them out into a net set downstream after the method described by Hobbs (1937 and 1940).

The collection of data regarding the angling catch was based primarily on the voluntary keeping of diaries by anglers who fished the Horokiwi. The stream was patrolled as often as possible on suitable days, particularly at weekends and at the beginning of the season, and all the anglers seen were contacted for the dual purpose of obtaining direct data regarding their catches and explaining to them the purpose of the diary scheme and asking for their co-operation. A special diary form was printed and distributed for this purpose; this had a cardboard cover of suitable size to go in the pocket or fishing bag, and was ruled on stout paper with columns for "date," "part of stream fished," "No. of fish kept," "No. of fish returned (under-sized and over-sized)," "marked fish," and "time fished (from.....to.....total.....)." With very few exceptions anglers showed considerable interest in the scheme, and freely undertook to supply the records asked for. It was found however that in many cases one or more reminders had to be sent at the end of the season, and that even then some of the records received were approximate or incomplete in some respects. In general however a very satisfactory degree of co-operation was obtained, and only about 10 per cent. of the anglers contacted failed to co-operate at all. Even in these cases some data were usually available from the original contact, and an estimate of the total season's catch in the Horokiwi by that angler could be made. A greater problem was presented by the anglers who were never contacted, although some very valuable help in this respect was received from some of the regular Horokiwi anglers, who either furnished data for others they encountered, or else advised the Fisheries Laboratory of their names and addresses. In later seasons a further check was provided by asking anglers encountered for the first time whether they had fished the Horokiwi in earlier years.

In the 1939–40 and 1940–41 seasons the stream was patrolled regularly and contact was made with most of the anglers who fished there. After field work on

the Horokiwi ended in October, 1941, postal contact with known Horokiwi anglers was kept up during the war years, and the field contacts were started again in 1946–47 and are still being maintained. Continuous data on the angling catch in the Horokiwi are therefore available from 1939–40 to the present time. The extension of this work beyond the period 1939–41 has enabled the effects of some of the events of that time on the angling catch of the later years to be investigated.

4. MOVEMENTS

Since this investigation was primarily aimed at obtaining an estimate of the productivity of the trout population in the Horokiwi stream, it was essential to find out how far this was an isolated and self-contained population. As it soon became apparent that there were differences in the productivity of various parts of the stream, it also became necessary to determine whether trout moved freely between the various regions, or whether there was only limited movement. If movement was extensive there would be virtually a single homogeneous population inhabiting the whole stream, but restricted movement would, in the extreme case, result in a series of isolated local populations.

It has already been pointed out that a complete river system was selected for this work, rather than a part of a larger system, in order to ensure that the trout population was, as far as possible, self-contained. Any interchange of trout between the Horokiwi and other waters must be limited either to the sea, or to other rivers entering the sea in the vicinity. The Horokiwi flows into the sea near the head of the Pahautanui inlet, which is an open shallow basin about 2 miles by $1\frac{1}{4}$ miles, connected with the open sea by a narrow winding channel. The only other stream of significant size which enters the inlet is the Pahautanui stream; this enters the sea only about half a mile from the mouth of the Horokiwi and is very similar to it in both size and type and contains a very similar trout population. The only waters therefore which are likely to have an interchange of trout with the Horokiwi are the Pahautanui stream and the Pahautanui inlet. Evidence regarding interchange with the Pahautanui stream is purely negative. A considerable number of trout have been tagged and released in the Horokiwi, but although the Pahautanui is relatively heavily fished by many of the same anglers who fish the Horokiwi no records have ever been received of any marked fish being caught there. This suggests that at least no extensive movement of trout from the Horokiwi to the Pahautanui stream takes place. There is no evidence regarding the reverse movement.

Although clearly defined migratory races of brown trout which would correspond to the sea-trout of Europe have not been recognized in New Zealand, some movement between the sea and fresh water seems to occur in most rivers containing brown trout, and in some places major river-mouth fisheries have developed (Hobbs, 1948). The possibility of such movements in the Horokiwi has therefore to be considered. It is believed that trout are occasionally taken in the Pahautanui inlet with seine nets, generally by amateur fishermen, but precise evidence is difficult to obtain, largely because the retention of net-caught trout is illegal. A limited amount of experimental netting carried out in the inlet near to the Horokiwi mouth yielded no trout. Among all the trout netted in the Horokiwi only one had the

characteristic appearance of a "sea-run" fish, with loose and very silvery scales and blackish fins; this was a fish of 35.2 cm., caught on 20th September, 1939, in section M 16, 1,500ft. above the river mouth. This fish, although superficially of the "sea-trout" type, was four years old and no larger than normal river fish of this age in the lower part of the Horokiwi. Its scales did not show any indication of a period of unusually rapid growth. All other trout caught in the Horokiwi, including many taken in the part of the stream influenced by the tide, have had a typical stream appearance. These data rather suggest that movement of trout between the sea and the Horokiwi is on a relatively small scale. At low tide the Horokiwi flows for a considerable distance spread out over the mud-flats, and this portion of the course would not then be normally habitable by trout of any size. This may perhaps tend to reduce movement of trout between the river and the sea.

Although the evidence regarding the movement of trout between the Horokiwi and the sea and nearby streams is rather incomplete, many more data are available regarding movement within the Horokiwi itself. These data are derived both directly from study of the movements of individual tagged fish, and indirectly from comparison of the characteristics of the fish taken in different parts of the river. During netting operations in the Horokiwi 76 tagged trout were recaptured. Of these 72 were recaptured in the zone in which they had been liberated; three were recaptured in an adjacent zone; and one was recaptured after travelling a comparatively long distance from Zone II M to Zone IV. The great majority of fish were recaptured either at the point where they were liberated or within a few hundred feet of it. The short distance travelled by most fish prior to recapture tends to be accentuated by the fact that most of the netting was concentrated at routine observation stations. This caused any fish which remained within the station where it was marked to have a much higher chance of recapture than one which travelled away, unless the latter happened to move into another of the routine stations. A separate analysis has therefore been made of the movements of fish liberated within a routine station and recaptured during later routine nettings, when the six stations were netted in full. Of the 42 such fish, all but two were found in the station where they were liberated; the two exceptions moved from M IV to M V and from R IV to R V. The distances travelled within the stations by the recaptured fish are summarized in Table 25. As the length of stream netted at one time was generally about 60 ft. to 120 ft., there is not always any difference in the distances actually travelled by fish recorded as travelling 0–50 ft., and by those recorded as travelling 51–150 ft. It is however perfectly clear from the table that even within the areas that are fully covered in every routine netting, most of the fish travel only a short distance, if at all. A slight error arises from the fact that the farther a fish travels the greater is its chance of passing out of the netting station. This error can be easily calculated if it is assumed that the tagged fish were originally distributed evenly throughout the station. The correction has been determined for an average length of station of 900 ft., and the results are shown in Table 25. It appears that 80 per cent. of the fish travel less than 250 ft. from the point of liberation before recapture; this supports the previous conclusion drawn from the uncorrected data that only a very small proportion of the fish ever move far enough to travel from one zone into another.

TABLE 25. The distance moved by tagged fish recaptured within the station in which they were liberated, and the estimated percentage of the population travelling various distances.

Distance Travelled (ft.)	0–50.	51–150.	151–250.	251–350.	351–450.	451–550.	551–650.	651–750.
Number of recaptures	24	5	2	1	2	0	1	0
Correction factor ..	1·000	1·125	1·285	1·500	1·800	2·250	3·000	4·500
Corrected percentage	58·6	15·1	6·3	3·7	8·8	0	7·0	0

The length of time between tagging and recapture varied from a few days to a maximum of 333 days, and several fish were recaptured two or three times. No correlation has however been found between the distance travelled and the length of time between tagging and recapture. Of six fish recaptured more than 200 days after tagging, four had not moved from the point of liberation, while the other two had moved upstream for 66 ft. and 200 ft. No seasonal movements were observed, and the few tagged fish which were recaptured while spawning were all taken at or near the point of liberation. Table 26 summarizes the movements of fish in different age-groups, each fish being placed in the age-group in which it fell on recapture, the year being assumed to begin on 1st October. It appears that there may be a tendency for older fish to travel more freely than first and second year fish, but further data are required on this point.

TABLE 26. The distances travelled prior to recapture by marked fish of various ages.

Age-group.	Distance Travelled (ft.).				
	0–150.	151–500.	501–1,000.	1,001–5,000.	5,001—
0 ..	5	1	0	0	0
I ..	27	2	1	4	2
II ..	12	6	0	0	0
III ..	6	1	0	1	0
IV–VI ..	3	0	2	1	0

The greatest distance recorded was travelled by a second-year fish which was tagged in Section M 210 in Zone II M on 27th November, 1940, and recaptured in Section R 551 in Zone IV on 10th June, 1941, having moved upstream a distance of 24,098 ft. in 195 days. This fish was again recaptured on 22nd October, 1941, without having made any further movement. All the other movements of more than 2,000 ft. have also been in an upstream direction. The only apparent exception was a fish tagged in Zone IV on 29th February, 1940, and reported by an angler from Zone II M on 21st April, 1940, a distance downstream of about 25,000 ft. Unfortunately the tag itself was lost before the number could be checked, and the record must therefore be regarded with reserve, in view of the lack of any similar authenticated movements.

Valuable indirect evidence regarding the extent of movement within the stream is provided by comparison of the size and growth of the trout in the various regions. As will be shown in detail later, the trout of any year-class taken at one time are

exceedingly uniform in size in any particular part of the stream, but very striking differences exist between the characteristic sizes in different regions. These differences persist throughout the life of the year-class, and are apparently the result of differences in the rate of growth in different parts of the stream. Consisent local differences of this sort could only occur in a stationary population, in which each fish is normally subject throughout its life to the same local growth-controlling influences. If any substantial movement of individual fish took place, the local growth effects would be masked, since the size of each individual would be the resultant of the growth it had made while in different regions. The uniformity of the fish of one year-class in any one region was normally so pronounced that when, as occasionally happened, a fish was taken which apparently belonged to the type characteristic of a different region, it contrasted very noticeably with the local type. Such occurrences were however very few, and the general uniformity supports the conclusion that the great majority of Horokiwi trout remain permanently in one short reach of the river.

If movement between the various parts of the Main Water and of the Road Branch is so limited, it seems unlikely that there will be any significant amount of interchange of fish between the Back Branch and the other portions of the stream. It appears justifiable therefore to neglect any effects due to interchange with the Back Branch in studying the production of trout in the Main Water and Road Branch of the Horokiwi. The relatively small amount of movement from point to point within the stream also supports the conclusion, based on negative evidence, that there is little interchange between the Horokiwi and neighbouring waters.

The final conclusion may then be reached that it is permissible for the purposes of this study to regard the trout population of the Horokiwi as being not only isolated and self-contained, but also composed of a succession of distinct local populations.

5. POPULATION

(a) Adults

The estimation of population has been attempted by somewhat different methods for two distinct parts of the life-cycle of the trout. The estimation of the numbers of adult fish has been based on marking and recapture methods, while the number of eggs and fry has been estimated both by determining the average egg production of mature females and applying this to the adult population estimates, and by counting redds and examining their contents.

The numbers of adult fish were estimated by determining from the recaptures of tagged fish the efficiency of the netting methods used, and by applying the result to the yields of the quarterly routine nettings of the standard stations. It was found that trout could not be netted sufficiently effectively to make this method practicable until they were several months old. The numbers of any year-class could not be estimated between the time of hatching of the fry and January of the following year. The present section deals with the estimates which have been made of the strength of each of the year-classes concerned at intervals from this time onwards.

The method of estimating a fish population by marking and releasing a number of fish, and subsequently determining by sampling the proportion of marked fish in

the population, was originally described by Petersen (1896) and has a very simple theoretical basis. The practical application however is fraught with many complications, and these become particularly evident when, as in the present study, the observations are spread over a comparatively long stretch of river, and the extent and frequency of netting for recaptures are severely limited by practical considerations.

The basic principles have been fully discussed by Ricker (1942) who has pointed out a number of possible sources of error in estimates derived in this way, and has considered means of dealing with them. His discussion, however, is largely restricted to the problem as it occurs in estimating the fish population of relatively small lakes. In rivers, where the population has a linear rather than a spatial distribution, additional complications arise, and these will be discussed below. In the earlier applications of the method all marking was completed before sampling for recoveries was begun. More recently the conditions of some investigations have made it necessary to carry out marking and sampling simultaneously, and this has required modifications of the original mathematical treatment. A solution of this problem has been put forward by Schnabel (1938). In the present instance the population estimates are based on observations which were carried on for a period of about two years, but a relatively long interval elapsed between successive marking and sampling operations, and therefore, since a number of successive population estimates is required, the original Petersen procedure with minor modifications is the more appropriate.

In the ideal case the population to be estimated is not only isolated but also consists of a single unit, and all the individuals wander freely throughout the area. In these circumstances the marked fish easily become scattered at random throughout the population, and the size of the population may be simply measured by determining the proportion of marked fish in a series of samples. This provides an estimate of the population which is not biased by the failure of the samples to be truly representative of the population as a whole. The reliability of the estimate can also be easily determined by standard statistical procedures, based on the number and size of samples.

If, however, each individual in the population is localized in its behaviour, and never strays far from one spot, the situation becomes much more complex. Under such conditions the only part of the population sampled in any recapture work is that which inhabits the particular area netted. If the number of marked fish which have been placed in that particular area is known, then an effective estimate of the population of that area can be made. This does not, of itself, provide any indication whatever of the population of the areas not sampled, nor, therefore, of the water as a whole. Other methods need to be used to convert the estimate of the population of the sampled area to one for the whole water. If the extent of the sampling areas, or the number of marked fish originally placed in them, cannot be accurately measured, then the estimate of the population of the sampled areas becomes less accurate, and, what is more important, its reliability can no longer be simply determined. The fiduciary limits cannot be calculated from the sampling data alone, but it becomes necessary to examine, by other methods, and to take into account, the probable errors in the basic quantities such as the size of the sampling area, and the number of marked fish placed in it.

In the Horokiwi the trout rarely move far from one place, and netting for the marking and recapture of fish was substantially restricted to a few sample areas. Conditions for the estimation of population were therefore essentially similar to the second case described above. Consequently the principle which has to be employed is the estimation of the population of sample areas by the marking technique and the extension of these results to the stream as a whole by other methods. The possible sources of error in this method which were mentioned in the previous paragraph are avoided in the present case, because the areas netted could be exactly defined and reproduced, since they consisted of the whole length of the stream between two known and recognizable points, and because the point of release of all marked fish was known.

Other possible errors are however produced by the relatively long time which elapsed between marking and recapture. This period was normally three months, and in the final interval between May and October, 1941, it was five months. In a period of this length the decrease in the proportion of marked fish in the area due to various causes could be substantial. The major possible causes are—differential mortality between marked and unmarked fish; movement of marked fish into or out of the area at a rate relatively different from that of unmarked fish; and loss of tags, leading to failure to recognize fish which had originally been marked.

Differential mortality could arise if attachment of the tag reduced the chance of survival of a fish by injury or otherwise placing it at a disadvantage. Despite the fact that the stream was constantly traversed in connection with various phases of this investigation, the number of dead or dying trout which were found was exceedingly small compared to the number which the population studies prove to have died during the same period. No satisfactory direct measurement of the relative mortality rates of marked and unmarked fish can therefore be made. None of the dead or dying fish which were found had been recently tagged, and the tagged fish when recaptured were almost invariably in as good condition as comparable untagged ones, and had shown normal rates of growth. It does not seem likely therefore that any pronounced increase in the mortality rate occurred as a result of tagging.

In the preceding section the movement of marked trout in the Horokiwi has been examined in detail. It was shown that although the Horokiwi trout generally remain in one place, a small proportion may move considerable distances. These movements may affect the proportion of marked fish in a station and so influence the estimates of population. The fish moving out of the area probably include both tagged and untagged fish in the proportions in which they are present in the station. The fish moving in will also include in theory both tagged and untagged individuals, but since the regular tagging stations formed only about 10 per cent. of the total length of the stream, a very small proportion of the incoming fish will be tagged, and in any case these can be recognized if recaptured. In practice only two fish were recaptured in a routine netting which had been tagged in another routine station, while 40 were recaptured in their station of origin. These movements of individual trout will therefore result in a decrease in the proportion of marked fish in a station, and will lead to a systematic error which must be corrected in an estimate of the population. This correction can be simply made by reducing the uncorrected estimate by a proportion equal to the proportion of

the fish originally marked which have moved out of the area. Although this proportion cannot be estimated directly from the available data, there are some observations which give an indication of its probable order of magnitude. Thirty-six tagged fish were recaptured in the quarterly routine nettings of the six main stations; only one of these was taken in a station different from that in which it was marked. Only about 9 per cent. of the water which a fish that had left its original station could occupy was netted on these occasions, i.e., this was the proportion included in the other five stations; this suggests that about a quarter of the fish tagged in each station had moved out by the time of the next routine netting. In the more thorough netting undertaken in April–June, 1941, only one of six tagged fish was recaptured outside its station of origin. Since in these operations about one-half of the stream was netted, this result also suggests that about a quarter of the tagged fish had left their original stations by that date.

The conclusion that about a quarter of the marked fish move out of a station between one routine netting and the next may be compared with the evidence presented in Table 25, that about 20 per cent. of the fish which remain within a station have travelled more than 250 ft. during the same period; the two results do not appear incompatible, although the recoveries within the stations would suggest that a rather lower proportion of fish left the station altogether. As a provisional estimate it is therefore assumed that 20 per cent. of the marked fish have moved out of the routine station before the next netting, and the estimates based on the proportion of the marked fish recaptured must therefore be reduced by a similar percentage.

During most of this work fish were marked only by the attachment of a tag to the dorsal fin. It later became apparent that some allowance would have to be made in estimating the population for loss of tags. To get some data on the rate at which these losses occurred, the fish of the 1940 year-class which were tagged in the period April–June, 1941, were further marked by the removal of the adipose fin. In the final routine netting in October, 1941, five fish without an adipose fin were caught. Two of these carried tags; two of the others had a scar on the dorsal fin where the tag had worked out; the fifth showed no trace of interference with the dorsal fin. Since not one of the 2,400 trout handled in the Horokiwi prior to October, 1941, had been observed to lack an adipose fin, it seems very probable that this was also one of the fish marked earlier in 1941. Thus, in this small sample 60 per cent. of the fish identifiable as having been tagged had lost their tags in a period of about five months. It is of course possible that other fish caught in October had also been tagged but had regenerated the adipose fin as well as losing their tags; studies made by other workers (Armstrong, 1949; Slater, 1949) on the extent to which this fin is regenerated after being carefully removed suggest, however, that this is unlikely.

Tagging on a significant scale was first carried out in the routine netting of July, 1940. In the routine netting of October, 1940, 15 fish were caught carrying tags which had been attached in July. A further six fish showed clear traces on the dorsal fin of having been previously tagged. Some of these six fish may have been among the few which had been tagged before July; on the other hand, the untagged fish caught in October may have included some which had been tagged in July which had lost their tags without a scar being formed. It may be assumed

therefore that in this sample of 21 fish tagged in July, 1940, about six, or 29 per cent., had lost their tags within three months. This result may be used to provide an approximate correction for loss of tags to be used in the estimation of population.

In the ideal case the original population in a given area at a given time may be estimated as the product of the number of fish originally tagged and the total number in the recapture sample, divided by the number of tagged fish in the sample. This estimate is of course subject to the sampling errors which may occur in the recapture sample, and these have been discussed by Ricker (1942). Where the sample is large, and the proportion of marked fish is high, so that the number of recaptures is also large, the probable sampling errors are small; but where the number of recaptures is small, as a result of either the small size of the sample, or of the low proportion tagged, the sampling errors may be considerable. In such a case it is desirable to reduce these errors as much as possible by suitable grouping of the results. In the present instance the basis for the estimate is provided by analysis of the recaptures in each routine netting of fish which had been tagged at the same station in the previous routine netting. The proportion of tagged fish in the recapture samples was small, being only 28 in a total of 299, or 9.3 per cent. Careful examination of the data is therefore necessary in order to obtain the best estimate of the proportion of tagged fish, and to determine its reliability. In the routine nettings, the routine stations were covered as thoroughly as possible, and all fish caught were tagged and released unless they were required for examination of stomach contents. The proportion of marked fish in these areas after each netting is therefore essentially a measure of the efficiency of the netting. This could be affected by several factors, such as the difficulty of the particular stretch of water, the water level, and the age or size of the fish. Some consideration must therefore be given to all of these in assessing the probable efficiency of netting.

TABLE 27. Test of the significance of the variation in the proportion of tagged fish taken in routine nettings at the different netting stations.

Station.	No. of Fish Caught.	No. of Fish Tagged (X).	p.	pX.
M II	22	1	0·045	0·045
M IV	63	6	0·095	0·570
M V	62	8	0·142	1·136
R II	13	1	0·077	0·077
R IV	89	11	0·124	1·364
R V	50	1	0·020	0·020
	299	28	$p = \frac{28}{299} = 0·093$	3·212

$$\chi^2 = \frac{3·212 - 28 \times 0·093}{0·093 \times 0·907} = 6·22$$

Table 27 shows the total number of fish taken in each of the routine stations in the four routine nettings between October, 1940 and October, 1941, and the number of these which bore tags attached at the previous routine netting. As would be expected, the proportion of marked fish in the catch varies considerably from station to station. To determine whether this variation is likely to have arisen as a result of random sampling, the value of chi-square for the series has been determined. The value obtained, 6.22, has a probability of occurring naturally of about 0.29 for five degrees of freedom. There is therefore no reason for refusing to accept the hypothesis that the efficiency of netting was similar at all stations.

To provide data on the effect of the age of the fish on netting efficiency, a comparison has been made between the results for the 1939 year-class, which was the youngest available throughout the period of observations, and the corresponding figures for the combined 1938 and earlier year-classes. In the series of observations under discussion, 201 fish of the 1939 year-class were taken, of which 18 carried tags which had been attached in the preceding routine netting; of the 52 older fish 8 still carried tags. Determination of chi-square for these results gives a value of 2.21, corresponding to a probability of chance occurrence of 0.14. The data therefore do not provide any adequate justification for rejecting the hypothesis that equal proportions of fish in the two age-groups had been tagged, and that netting was equally efficient in each case.

Table 28. The total number of fish and the number carrying tags attached at the previous routine netting caught in each routine netting after July 1940; the results for the 1939 year-class and for older fish being shown separately.

Year-class	Date tagged	July, 1940.	Oct., 1940.	Jan., 1941.	May, 1941.
	Date recaptured ..	Oct., 1940.	Jan., 1941.	May, 1941.	Oct., 1941.
1938 and earlier	Number caught.. ..	24	13	11	4
	Number previously tagged	6	0	1	1
	Ratio	0·25	0·00	0·09	0·25
1939	Number caught.. ..	81	62	42	16
	Number previously tagged	9	3	3	3
	Ratio	0·11	0·05	0·07	0·19

The influence of season, and of age of fish, on the efficiency of netting can be tested from the data given in Table 28. This shows separately the results for each netting for fish of the 1939 year-class and for older fish. There is reasonably good agreement between the proportions for fish of different ages. The proportion of tagged fish is somewhat less in the nettings of January and May, 1941 than in the other two. It seems unlikely however that this is due to the nettings of October, 1940 and January, 1941 being relatively inefficient; the number of fish actually caught and tagged in October, 1940 was very little less than that of July, 1940 which led to the relatively high proportion of tagged fish in the following October. The best hypothesis therefore appears to be that netting was equally efficient on the four occasions. This conclusion is supported by the determination of chi-square. The value obtained from the eight samples, 11.7, has a probability of about 0.12, and therefore lies well within the commonly accepted limits of significance. The

mean value for the proportion of marked fish shown in the table, 0.103, has therefore been accepted as the uncorrected value for the efficiency of netting in all seasons and zones.

It has been shown that the proportion of tagged fish in each station is reduced between one routine netting and the next by loss of tags and by emigration. The best correction for these effects was found to be to increase the proportion of marked fish found in the sample by 20 per cent. and 30 per cent. respectively. The best estimate of the efficiency of netting therefore appears to be 0.15.

The reliability of these estimates of netting efficiency may be examined by entering the results given in Table 28 in a table giving the range of the probable composition of the population for various samples for given fiduciary limits. The table given by Snedecor (1946) for the 95 per cent. confidence limits shows that the uncorrected estimate of netting efficiency can be stated with 95 per cent. confidence to lie within the range of 0.07 to 0.14. The corresponding corrected values are 0.10 to 0.21. An alternative method of estimating the probable errors in this method of population measurement is given by Gross (1950) without derivation. In this method, if n is the number of marked fish recaptured, the limits of the population for 95 per cent. confidence are those corresponding to recapture numbers of $n - \sqrt{n}$ and $n + 2\sqrt{n}$. Applying this method to the data of Table 28 we get a range for the uncorrected estimate of netting efficiency of 0.07 to 0.12. The lower limit of this is the same as that given by the method adopted above while the upper limit is slightly less.

When the efficiency of netting is known, the actual population in any region which has been thoroughly netted can be determined. In order to obtain estimates of the total population of the various zones, and of the stream as a whole, it is necessary to know the relation between the population density of the routine netting stations and the average densities of the larger regions. A basis for this is provided by the results of the netting operations carried out between 22nd April and 15th June, 1941. On this occasion the stream was divided into a series of approximately equal stretches and alternate ones were netted. Table 29 shows the total number of fish of each year-class taken in each of the stations used on this occasion; from this the average density of the population in numbers per 10,000 sq.-ft. is determined for each station and for each zone, and the data given in Table 6 are used to compute the total population of each zone. This is then allocated between the year-classes in accordance with their proportions in the actual catches. Both the density and the composition of the population showed a reasonable degree of consistency from zone to zone. The most striking variations in density were in the two regions of relatively sparse population, at the mouth of the stream in Zone I, and about the boundary between Zones II R and III. The population also showed distinct and fairly consistent variations in age composition, and particularly in the relative numbers of the 1940 and 1939 year-classes. The 1940 fish appeared relatively most numerous in Zone I and least numerous in Zone IV. The 1939 fish, on the other hand, were particularly abundant in Zone IV. Older fish were relatively numerous in Zone IV and in the upper part of Zone I. In order to estimate the populations of the zones at other times from the results of netting only the six routine stations, the average density for the whole of each

TABLE 29. The numbers of fish of each year-class, caught in each station, in the netting of April–June, 1941, and the total numbers estimated to have been present.

Zone.	Netting Station.	Equiv. Routine Netting Station.	Number Of Fish Taken Year-class. 1940.	1939.	1938.	1937.	1936.	1935.	1934.	Total	Est. Total. Number Present.	No. per 10^4 sq. ft., Station	Zone.	Estimated Number in Zone. Total.	Year-class. 1940.	1939.	1938.	1937.	1936,	1935.	1934.
I ..	MA ..		5	5	..	..	..	..	..	10	66	40									
	MB ..		30	2	..	..	..	..	..	32	213	137									
	MC ..	M II	42	4	..	..	..	..	..	46	307	239									
	MD ..		51	6	..	2	1	..	1	61	408	279									
	ME ..		50	4	2	1	..	1	..	58	386	295	189	2,942	2,530	299	28	43	14	14	14
II M	MF ..		54	12	1	..	..	..	..	67	447	342									
	MG	M IV	34	..	1	..	..	..	..	35	233	211									
	MH ..		99	25	1	..	..	..	..	125	833	573									
	MI ..	M V	60	17	1	1	..	..	..	79	526	616	430	3,920	3,164	692	52	12	..	..	..
II R	RA ..		45	8	..	..	..	..	..	53	353	255									
	RB ..		5	3	..	1	1	..	..	10	65	44	147	913	726	159	..	14	14	..	..
III ..	RC ..	R II	5	5	2	..	..	..	..	12	79	49									
	RD ..		20	11	..	..	..	..	..	31	206	152									
	RE ..		24	29	1	..	..	..	..	54	359	316	156	1,363	689	632	42	..	..	..	..
IV ..	RF ..		6	22	2	3	..	..	..	33	220	191									
	RG ..	R IV	13	14	1	2	..	..	1	31	205	195	192	800	237	452	37	62	..	..	12
V ..	RH ..	R V	18	10	1	..	..	..	..	29	193	190	190	248	154	85	9	..	..	..	..
	TOTALS ..		561	177	13	10	2	1	2	766	5,099	..	..	10,186	7,500	2,319	168	131	28	14	26

zone has been compared with the density of the routine stations lying within it. In Zone II M the mean of stations M IV and M V has been used for this comparison. A satisfactory level of agreement was found in Zones II M, IV and V; in Zone I the average density was rather less than in station M II and a conversion factor of 0.8 seems appropriate. In Zone III there was a considerable discrepancy due to the fact that the routine station R II lay within the region of sparse population mentioned above. General observations suggested that this type of distribution was a regular feature of the zone, and a conversion factor of 3.2 has therefore been used to estimate the mean density of the Zone III population on other dates. No routine stations lay within Zone II R, and it appears that this zone had a very unequally distributed population; any estimate of its population must therefore be considerably less reliable than those of other zones. In order to provide an indication of this population, its density has been estimated at one third of the mean of stations M IV and M V.

Estimates of the population made in this way for a number of successive dates are shown in Table 30. This shows the number of fish of each year-class which were taken in each zone in the routine nettings of July, 1940, October, 1940, January, 1941, and October, 1941, as well as in the extended netting of April to June, 1941. It also shows the number of fish of each year-class in each zone as estimated by the methods outlined above. The results for the 1936, 1937 and 1938 year-classes have been smoothed by the same method as was previously applied to the bottom fauna estimates. The numbers of fish caught belonging to the 1934

TABLE 30. The numbers of fish of each year-class caught and estimated to have been present in each zone at each routine netting.

Year-class.	Date.	Number caught in zones							Estimated total populations in zones.						
		I.	IIM.	IIR.	III.	IV.	V.	Total.	I.	II M.	II R.	III.	IV.	V.	Total.
1940	Jan. 41	99	69	..	11	21	12	212	6,330	2,250	500	1,950	800	170	12,000
	May 41	178	247	50	49	19	18	561	2,520	3,175	725	700	240	150	7,500
	Oct. 41	2	27	..	1	13	5	48	140	800	180	170	550	60	1,900
1939	July 40	12	62	..	4	16	14	108	750	1,875	425	675	600	175	4,500
	Oct. 40	..	37	..	3	25	16	81	650	1,130	250	520	950	200	3,700
	Jan. 41	14	28	..	2	13	10	67	900	920	200	350	490	140	3,000
	May 41	21	54	11	45	36	10	177	300	680	160	625	450	85	2,300
	Oct. 41	0	6	..	0	4	7	17	0	175	40	0	170	90	475
1938	July 40	5	4	..	3	6	1	19	300	190	40	425	250	15	1,220
	Oct. 40	..	6	..	3	7	0	16	310	200	40	450	270	15	1,285
	Jan. 41	2	2	..	0	3	1	8	80	50	10	120	70	5	335
	May 41	2	4	0	3	3	1	13	40	25	5	60	35	2	167
	Oct. 41	0	2	..	0	0	0	2	18	12	3	25	15	1	74
1937	July 40	1	4	..	0	10	1	16	140	80	25	0	355	10	610
	Oct. 40	..	0	..	0	6	1	7	65	40	10	0	175	5	295
	Jan. 41	2	1	..	0	2	0	5	55	30	10	0	145	5	245
	May 41	3	1	1	0	5	0	10	30	17	5	0	75	3	130
	Oct. 41	0	0	..	0	0	0	0	0	0	0	0	0	0	0
1936	July 40	0	0	..	1	1	1	3	10	0	10	130	60	10	220
	Oct. 40	..	0	..	0	1	0	1	2	0	2	24	10	2	40
	Jan. 41	0	0	..	0	0	0	0	2	0	2	20	10	1	35
	May 41	1	0	1	0	0	0	2	2	0	2	18	7	1	30
	Oct. 41	0	0	..	0	0	0	0	0	0	0	0	0	0	0
1935	July 40	0	1	..	0	0	0	1	..	..	..	..	..	..	40
	Oct. 40	..	0	..	0	0	0	0	..	..	..	..	..	..	32
	Jan. 41	0	0	..	0	0	0	0	..	..	..	..	..	..	12
	May 41	1	0	0	0	0	0	1	..	..	..	..	..	..	6
1934	July 40	1	0	..	0	0	0	1	..	..	..	..	..	..	40
	Oct. 40	..	0	..	0	0	0	0	..	..	..	..	..	..	32
	Jan. 41	0	0	..	0	0	0	0	..	..	..	..	..	..	12
	May 41	1	0		0	1	0	2	..	..	..	..	..	..	6

and 1935 year-classes were so small that only very approximate estimates of their populations could be made. Only estimates for the entire population of the stream are shown in the table, and these have been calculated to bear the same relation to the estimated combined total of the 1936, 1937 and 1938 year-classes as was found in the numbers of fish actually caught.

The estimates of the 1940 year-class for January, 1941 are almost certainly considerably below the true value, since these fish, which were then generally between 7 cm. and 13 cm. in length, were less efficiently netted than were the larger fish. It is not however possible to determine how far the figures given in Table 30 may be in error.

It has already been shown that errors in estimations of populations by the methods used in this work can arise either from errors in the determination of the proportion of fish taken, or from sampling errors in the particular collection. The reliability of the estimated netting efficiency has been discussed above, but further consideration must be given to the nature and extent of the sampling errors. It is being assumed in the present instance that the netting efficiency is 0.15, i.e., that in the average case the number of fish caught forms 0.15 of the total number in the area. The mechanism by which this proportion is selected depends upon the netting technique used, and upon the behaviour of the fish in relation to it. Although other hypotheses relating the chance of catching each fish with such factors as its physiological state are possible, the most reasonable one would appear to be that every individual fish had an equal chance of evading the nets, and that the catching of fish taken is therefore a true sampling process. Such a mechanism can be subjected to statistical analysis, and the magnitude of the errors which would arise in this way may be determined. If the probability of capturing any one individual in a total population of n is given by p, then the number captured (x) in a series of separate netting operations (if the initial population is restored to n each time) will be distributed in accordance with the expansion of the binomial $(p + q)^n$, where $p + q = 1$. In most studies of fiduciary limits in relation to such a distribution, the data provide values of x and n and the reliability of the estimate of p is being examined. For this purpose the charts of Clopper and Pearson (1934) or the table of Snedecor (1946) may be used directly. In the present case however the value of x is known; that of p is assumed (0.15), and we are concerned with estimating the value of n. This may be approached in two ways; in one, two values of n may be found such that the actual value of x lies on the opposite boundaries of the zones corresponding to the desired fiduciary limits for the given value of p. These values of n may be approximately determined by interpolation in the charts or tables mentioned above. The other approach lies in the determining of the desired fiduciary limits from examination of the distribution of n for fixed values of p and x. Since the distribution is binomial the frequency of x captures from a population n is given by—

$$\frac{n\ (n-1)\ \ldots\ (n+1-x)}{\lfloor x} \cdot p^x\, q^{n-x}$$

Since x is a constant and n the variable this may be rewritten:

$$\frac{p^x}{\lfloor x} \cdot \frac{n}{\lfloor n-x} \cdot q^{n-x} \text{ where } \frac{p^x}{\lfloor x} \text{ is a constant.}$$

Thus the relative frequencies of the different values for the total population for a given value of x are given by the terms of the above series for successive values of n. It should be noted that the probabilities thus obtained have a sum greatly in excess of unity; they have therefore to be scaled down to make their sum equal to one in order to convert them into a true probability series. If this is done the cumulative totals can be calculated, and the limits for any desired level of confidence can then be determined. These limits give the range within which the selected percentage of populations would fall if all samples containing x individuals were selected from an infinite number of samples taken with a probability of p from populations of all sizes. This series can therefore be used to determine the limits of the estimated population for any desired degree of confidence when a sample of known size is taken with a known probability of catching each individual fish.

Two series of this kind have been calculated; those for $x = 5$, and $p = 0.1$, and for $x = 2$, $p = 0.133$, the limits for 95 per cent. confidence for n are respectively 22 to 112, and 4 to 51. Interpolation in the tables of Snedecor (1946) for these values of p yields values of n which have the given values of x at the 95 per cent. confidence limits as 18 to 120, and 5 to 54 respectively. It appears therefore that, at least for small values of x, the limiting values of n for 95 per cent. confidence are very similar for the two criteria suggested above. Although the fiduciary limits obtained from the distribution of n for given values of p and x are theoretically preferable, they have to be specially computed, whereas the values for the other method can be obtained from existing tables. In view of the apparent close similarity in the results the second method will be used in this work on account of its greater convenience.

The estimates of zone and whole stream populations developed in this study are based primarily on the populations of the representative netting stations as determined from the numbers of fish actually caught, and the indicated netting efficiency of 0.15. As has been shown the size of the probable sampling errors in this procedure can be determined directly from the number of fish actually caught. The approximate range of the 95 per cent. confidence limits in relation to the estimate of the total population is given in the following table for samples of various size:

5 fish	+ 150 % to − 65 %
20 fish	+ 50 % to − 35 %
50 fish	+ 33 % to − 22 %
100 fish	+ 22 % to − 15 %

It appears that the probable sampling errors in the population estimates for the relatively numerous 1939 and 1940 year-classes generally lie within limits of about 20 per cent. to 30 per cent., but that the relative error increases for the older and less numerous year-classes, and could be as high as − 75 per cent. to + 250 per cent. for the scarce 1936 year-class.

Finally, there may be systematic errors in the estimates of zone and total populations, due both to inaccuracies in the estimate of the relation between the areas of the routine stations and of the zones as a whole, and to variations from time to time in the relation between the density of the population in the station and that of the zone as a whole. The probable errors in the estimates of the areas of the various parts of the stream have already been shown to be about ± 5 per cent., and they are therefore negligible compared with the sampling errors in the population estimates. Assessment of the errors due to the variation of relative density is more uncertain. Some indication is provided by examination of the variation from time to time in the size and composition of the samples caught in the different stations. This appears to show on the whole a reasonably consistent relation between the stations, and this rather suggests that the errors due to changes in relative density may be fairly small in comparison with the sampling errors.

Considerable discussion has now been devoted to the extent of the probable errors in the estimates which are set out in Table 30 of the size and structure of the Horokiwi trout population. Owing to the complexity of the factors which have been considered a summary of the principal conclusions seems to be desirable.

1. It is statistically satisfactory to assume that the proportion which was tagged of fish present was constant for all stations and all routine nettings.

2. The mean proportion of fish found to be carrying tags attached at the previous routine netting was 0.103.

3. About 20 per cent. of the fish tagged in a station probably left it before the next routine netting, and about 30 per cent. lost their tags.

4. The efficiency of netting was therefore taken to be 0.15; consideration of the size of the samples indicates that the 95 per cent. confidence limits for this estimate were about 0.10 to 0.21, i.e., — 33 per cent. to + 40 per cent.

5. Reliability of the estimates of the populations of the different zones will depend partly on the accuracy with which the sampling stations are representative of the zones. The highest degree of accuracy in this respect is obtained in Zones II M, IV and V, while relatively serious errors might occur in Zones II R and III. Zone I occupies an intermediate position.

6. The estimate of the 1940 year-class in January, 1941 is almost certainly substantially below its true value on account of the inefficient netting of these small fish.

7. The sampling errors which arise when a population is netted with a probability of 0.15 of catching each individual are examined. Probable errors arising in this way are about ± 25 per cent. for the 1939 and 1940 year-classes, increasing to about — 75 per cent. to + 250 per cent. for the 1936 year-class.

8. Systematic errors due to inaccurate measurement in the areas of stations and zones are negligible.

9. Systematic errors due to variation from time to time in the relative densities of station and zone populations are believed to be unimportant, particularly in the more consistent zones.

It appears therefore that the major sources of error in the population estimates arise from the sampling errors both in the determination of the efficiency of netting and in the estimation of the size of the population which yields a given catch. For the more numerous age-groups, the former errors are the more significant, but they are greatly exceeded by the catch errors for the older and less numerous fish. The best estimates available appear to have a probable error of about ± 50 per cent. for 95 per cent. fiduciary limits.

(b) Egg and Fry Production

This may be estimated by the determination, in each year, of the number of spawning females of each size, and by examination of the relation between the size of fish and egg production. In the preceding section estimates have been made of the number of fish of each year-class living in each zone at various times. From these results an estimate of the number of mature females may be made by using data regarding the proportion of females in the population and the proportion of these which become mature in each year of age. The sex of all fish killed was recorded whenever it could be determined with certainty. In all, 146 males and 159 females were identified. The probability of at least this difference being obtained from a population containing equal numbers of males and females is 0.5, and there is therefore good reason to accept an equal distribution of the sexes as a working hypothesis.

All fish examined were also classified according to whether or not they would spawn or had spawned during that year. It was found that this could be determined by examination of the gonads for fish of age-group I from December onwards, and in older age-groups all fish caught could be classified as either immature, mature, or spent. The number and percentages of immature and mature fish in each age-group are shown in Table 31; in this case the term "mature" includes spent

Table 31. The numbers and percentages of immature and mature fish of each sex in all age-groups examined.

Age-Group.	Males.				Females			
	Immature.		Mature.		Immature.		Mature.	
	No.	%	No.	%	No.	%	No.	%
I ..	11	*20*	43	*80*	6	*9*	62	*91*
II ..	0	*0*	14	*100*	1	*5*	18	*95*
III ..	0	*0*	9	*100*	0	*0*	12	*100*
V ..	0	..	0	..	0	*0*	1	*100*

fish. The data show that a surprisingly high proportion of females mature at the end of their second year, and that beyond this age virtually all are mature. As the population data are being examined on a zonal basis, it is necessary to consider

whether these results apply generally in the Horokiwi. For this purpose the largest group, that of 62 females of the 1939 year-class examined in 1941, was split up according to its zones of origin. Application of a chi-square test to the results showed a probability of 0.5 of the same degree of variation occurring by chance if the same proportion of fish were mature in the population of all zones. The mean value of 91 per cent. maturity among age-group II females may therefore be applied with confidence in all zones.

These data provide a basis for estimating the number of mature females in each zone in each spawning season. To determine the total egg production, it is necessary to know the average egg content of the females of each group. For this purpose the number of developing eggs was counted in every female examined which was sufficiently far advanced. Since the number of eggs varies with the size of fish it was necessary to study the nature of the relationship. It was found that the relation between egg-number and weight was definitely curvilinear, but that egg-number when plotted against fork length, as in Fig. 3, gave a reasonably good fit to a straight line. Some of the fish examined were taken as much as three or four months prior to spawning while they were still actively growing; it therefore seemed desirable to convert all lengths to approximate lengths at spawning time, and 1st July was taken as a representative date for this purpose. This was done

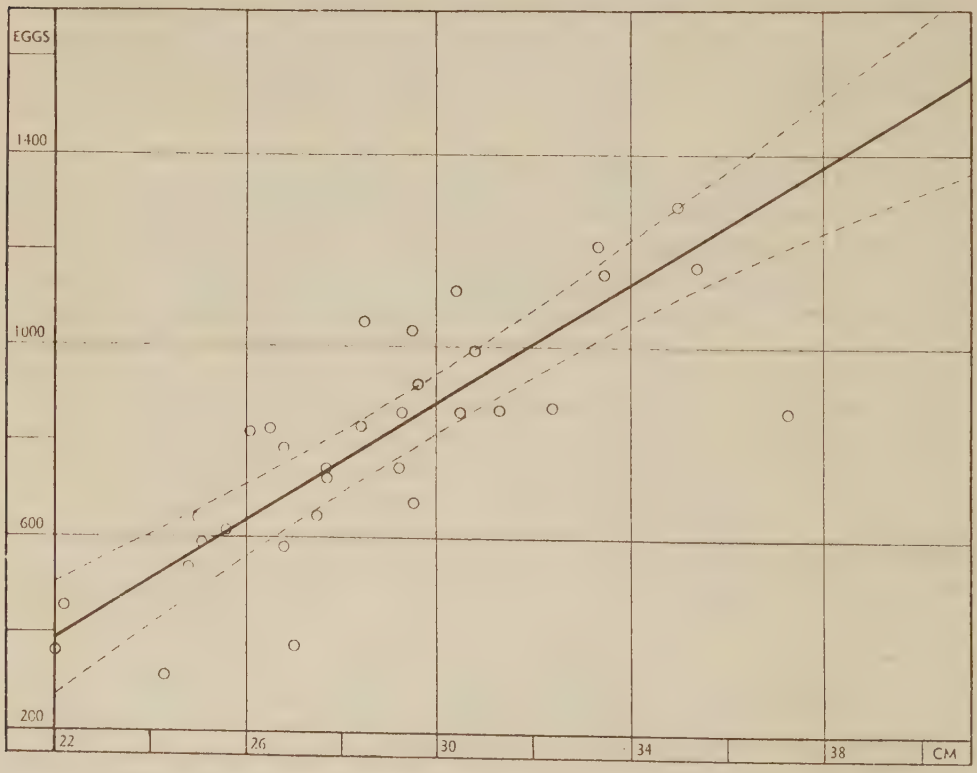

FIGURE 3. The number of eggs in each female fish examined plotted against the fork length. The solid line is the regression line referred to in the text and the dotted lines mark the boundaries, for 95 per cent. confidence, of the mean egg production at any length.

by multiplying the actual length at capture by the ratio between the mean length of that year-class in that zone on the same date and on 1st July. The regression line of number of eggs on length was calculated from these results, and was found to be:—

$$N = 61.24\ (L - 15.65)$$

where N = number of eggs, and L = fork length at spawning time in cm. This line differs slightly from that given in a previous summary of this work (Allen, 1946) where a line had been fitted approximately by eye, but over the most important part of the range the calculated egg-numbers differ by less than 10 per cent. This relation has been compared with that obtained by Smith (1947) for a collection of data from *Salvelinus fontinalis*; while these fish appear to contain rather more eggs, the line obtained for the Horokiwi trout lies well within Smith's limits of one standard error of estimate and the line for *S. fontinalis* lies over most of the range just within the 95 per cent. confidence limits for the

TABLE 32. The number of mature females and the computed egg production for each year-class in each zone in the year 1940.

Year-class.	Zone.	No. of Mature Females.	Mean Length (cm.).	Average Egg Content.	Total Egg Production.
1938	I	135	33·0	1,060	143,100
	II M	85	30·0	880	74,800
	II R	18	30·0	880	15,850
	III	191	28·0	760	145,150
	IV	113	23·5	480	54,200
	V	7	27·5	730	5,100
	Total	549	..	..	438,200
1937	I	66	39·0	1,430	94,350
	II M	38	33·0	1,060	40,300
	II R	12	33·0	1,060	12,700
	III	0	..	..	0
	IV	169	27·0	700	118,300
	V	5	31·0	940	4,700
	Total	290	..	..	270,350
1936 and earlier	I	25	41·0	1,550	38,750
	II M	20	39·0	1,430	28,600
	II R	5	39·0	1,430	7,150
	III	65	35·0	1,185	77,050
	IV	30	28·0	760	22,800
	V	5	34·0	1,125	5,650
	Total	150	..	..	180,000
	Grand total	989	..	..	888,550

TABLE 33. The number of mature females and the computed egg production for each year-class in each zone in the year 1941.

Year-class.	Zone.	No. of Mature Females.	Mean Length (cm.).	Average Egg Content.	Total Egg Production.
1939 ..	I	135	32·2	1,015	137,000
	II M ..	330	29·5	850	280,500
	II R. ..	72	29·5	850	7,650
	III	281	25·0	575	162,000
	IV	203	23·5	480	97,500
	V	38	27·0	700	29,600
	Total	1,059	..	..	714,250
1938 ..	I	19	38·0	1,370	26,050
	II M ..	12	34·0	1,125	13,500
	II R ..	2	34·0	1,125	2,250
	III	28	31·0	940	26,300
	IV	17	26·0	635	10,800
	V	1	31·0	940	950
	Total	79	..	..	79,850
1937 .. and earlier	I	19	41·0	1,550	29,450
	II M ..	11	39·0	1,430	15,700
	II R ..	3	39·0	1,430	2,900
	III	9	35·0	1,185	10,700
	IV	41	28·0	760	31,150
	V	2	34·0	1,125	2,250
	Total	85	..	..	92,150
	Grand total ..	1,223	..	..	886,250

Horokiwi data. The data from the Horokiwi do not show any indications of significant differences in the relation between egg-content and size for different age-groups or different parts of the stream.

In Tables 32 and 33 the egg production of each year-class in each zone is calculated by inserting the appropriate mean lengths obtained from the growth studies in the above formula, and multiplying the result by the estimated numbers of mature females obtained from the data in Tables 30 and 31. In the 1940 data in Table 32 the population estimates are based on the results of the July routine netting, which coincided closely with the spawning season. The 1941 data in Table 33 are based on the estimate of the population in May of that year. A substantial decrease in the population apparently occurred between May and October, and this renders the estimate of the spawning population somewhat uncertain. Most of the heavy floods, which may have been a possible cause of the reduction in the population, occurred after the spawning season and it therefore

seems best to accept the May figures as an estimate of the spawning population, but to regard them as being possibly somewhat too high.

Some consideration should be given to the errors involved in these estimates of egg production. The final figures are based on two separate estimates each involving sampling errors. These are the estimates of the number of spawning females and of the egg production per female. Errors in the total population estimates have already been discussed at length. Further sampling errors arise in determining the proportion of females in the population, and the proportion of these which are mature in each age-group. Reference to the table of fiduciary limits given by Snedecor (1946) shows that for 95 per cent. confidence the proportion of females in the population lies between 45 per cent. and 55 per cent. This imposes an additional error of ± 10 per cent. on the estimate of the number of females. Sampling errors will also occur in the estimate of the proportion reaching maturity at a given age, and reference to the same table shows that for the various age-groups the range of the percentage probable error of this estimate for 95 per cent. confidence is:

Age-group I	−11% to +7%
„ II	−23% to +5%
„ III	−22% to 0%

Since the estimates themselves show the progressive increase with age which would normally be expected, errors of more than 10 per cent. seem to be unlikely in any age-group, and in the older groups the error can only lie in a negative direction.

The methods set out by Snedecor (1946, p. 120) can be used to determine from the original data the probable error for any desired fiduciary limits in the estimate of the egg production of an average female of a given size. These limits vary with the size of the fish and for 95 per cent. confidence vary from ± 7 per cent. for fish about 30 cm. to ± 14 per cent. for the largest and smallest spawning fish encountered.

Thus, in estimating egg production three additional sampling errors each of the order of ± 10 per cent. are imposed on the original probable errors of ± 50 per cent. in estimates of total population. Aroian (1947) has shown that the standard deviation of the product of two normally distributed uncorrelated variables of means m_1 and m_2 and standard deviations σ_1 and σ_2 is given by:

$$\sigma m_1 m_2 = \sqrt{m_1^2\sigma_2^2 + m_2^2\sigma_1^2 + \sigma_1^2\sigma_2^2}$$

This result may be extended for a greater number of variables, and the standard deviations may be expressed as proportions of the means in the form $m_1 f_1$, $m_2 f_2$ etc. For the product of four variables we then get:

$$\sigma = m_1 m_2 m_3 m_4 \sqrt{\Sigma f_1^2 + \Sigma f_1^2 f_2^2 + \Sigma f_1^2 f_2^2 f_3^2 + \Sigma f_1^2 f_2^2 f_3^2 f_4^2}$$

so that the relative deviation of the mean product is given by:

$$\sqrt{\Sigma f_1^2 + \Sigma f_1^2 f_2^2 + \Sigma f_1^2 f_2^2 f_3^2 + \Sigma f_1^2 f_2^2 f_3^2 f_4^2}$$

In the present case an approximation to the range of probable error can be obtained by assuming that the four estimates involved are all normally distributed, and in this case they will have standard deviations approximately equal to half the range of the 95 per cent. confidence limits. The standard deviation of the final

result can therefore be obtained by inserting $f_1 = 0.25$, $f_2 = f_3 = f_4 = 0.05$ in the above expression. From this it appears that the relative deviation of the final estimate is approximately 0.266 and the range of the 95 per cent. fiduciary limits is therefore ± 53 per cent. The additional errors introduced in the computation of egg production from the adult population estimates are evidently so small as to have little effect on the range of the fiduciary limits, and the reliability of the estimate of egg production is substantially of the same order as that of the population size at other points in the life-cycle.

Some check on the reliability of the estimate of the distribution of egg production between the zones can be obtained by comparing the estimated egg production of each zone with the estimated numbers of resulting fish in the following January. This comparison can only be made for the 1940 spawning season, and the relevant data are given in Table 34. This shows the estimated numbers of eggs produced in each zone in 1939, and the estimated numbers of resulting fingerlings in January, 1940. The correlation coefficient between the two sets of data is 0.76, which approaches the 5 per cent. level of significance for the number of degrees of freedom involved. This appears to provide some support for the allocation of egg production between the zones by the methods used above.

These estimates of egg production refer to the numbers of eggs contained in the female fish before spawning commences. A variety of factors operate to reduce the numbers of fry actually produced from these eggs. The first of these is the failure of the fish to shed all their eggs. All spent fish killed were carefully examined for unshed eggs, although, unfortunately, only nine such fish were available. These contained altogether a total of 25 unshed eggs. Their estimated total egg content as calculated from the formula set out above was 6,830, of which the unshed eggs would form 0.37 per cent. Hobbs (1948) who examined another small sample of New Zealand brown trout found that 0.6 per cent. of the eggs were unshed. A sample of 46 spawning brown trout examined in American waters by Brown & Kamp (1942) contained unshed eggs to the extent of 0.38 per cent. of the new eggs present. There is no indication in this instance as to the proportion of fish which had actually spawned before, and consequently 0.38 per cent. would be a minimal estimate of the proportion which are not shed. It is also possible that some unshed eggs may be absorbed or expelled from the body cavity after true spawning is over and all the above figures therefore represent minimal estimates of the proportion of eggs not shed. It would appear however that a working estimate of 0.5 per cent. for unshed eggs is reasonable. This is negligible when compared to the wide fiduciary limits of the present estimates of egg production, and may be ignored.

Some eggs are lost through failure to lodge in the redds during spawning. Such losses are not easily estimated but Hobbs (1948), from consideration of the New Zealand data, arrived at a figure of 2 per cent. as a working estimate of these losses. Some indication of the extent to which eggs become available to feeding trout, either by failure to lodge in the redd, or by interception, can be obtained by the examination of stomach contents of trout taken during the spawning season. Of 137 trout examined between May and September inclusive, only three contained trout eggs, and in each case only a single egg. Two of these were taken

in July in the middle of the spawning season, but the third was taken on 29th September, 1940, more than a month after spawning is normally ended. This suggests that this egg had somehow become dislodged by disturbance of an old redd, although no such happening was observed in the vicinity.

While losses due to the failure of eggs to lodge successfully in the redds seem generally small, the work of Hobbs and others has shown that greater losses occur through infertility or death of the eggs in the redds. In a survey of a number of New Zealand river systems, Hobbs (1940) found that the mean losses from these causes varied in the different river systems between 3.2 per cent. and 29.3 per cent. of the eggs deposited. The individual losses in redds which had reached the alevin stage varied between 0 and 82 per cent., but the mean loss was only 11 per cent. and in 84 per cent. of the redds examined the loss was less than 20 per cent. Only a few redds have been excavated in the Horokiwi but these showed losses ranging from 23 per cent. to 92 per cent. of the eggs deposited. Losses from these causes therefore seem likely to be relatively high in the Horokiwi, and may be greater than in most of the rivers examined by Hobbs.

In some waters the disturbance of redds and the displacement of eggs by later spawners appears to be a significant cause of loss. This may have considerable significance in streams where the area of suitable stream bed is very limited; it is likely to be of less significance however in a stream such as the Horokiwi, where suitable spawning sites are abundant, and where few fish move more than a short distance in order to find a good spawning area. Even under these conditions, however, there seems to be a significant amount of concentration of redds, and hence of superimposition; this may be a result of gregarious tendencies on the part of spawning fish.

TABLE 34. The number of redds observed, the estimated number of eggs produced, and the estimated number of resulting fry in the following January for each zone for the 1940 spawning season.

Zone.	Number of Redds observed on								Estimated Egg Production.	Estimated No. of 1940 Year-class in Jan., 1941.
	7 June.	15 June.	20–21 June.	27 June.	12–15 July.	30–31 July.	13 Aug.	21 Aug.		
I	5	*18*	45	47	54	60	62	62	276,200	6,330
II M	9	*36*	39	66	92	100	104	104	143,700	2,250
II R	..	*17*	17	*30*	35	43	45	*52*	35,700	500
III	..	*11*	17	..	29	52	57	*61*	222,200	1,950
IV	..	*2*	16	*16*	41	46	51	*55*	195,300	800
V	..	*6*	8	*16*	19	22	22	*22*	15,450	170
Total ..	14+	90	142	175+	270	323	341	356	888,550	12,000

In 1940 good weather prevailed throughout the spawning season and no floods of sufficient size to disturb the stream bed occurred. The stream was closely examined at intervals of about ten days from 7th June until 21st August, and the position and condition of every redd seen were recorded by the methods described earlier. On most visits the whole length of the stream was examined, but on a few occasions only a portion of the stream was searched and the total numbers in each zone at that date were estimated. The results are shown in Table 34, the estimated numbers being given in italics. Wherever an estimated number is shown at least

part of the zone was examined on the date in question. The results show that spawning occurs in all parts of the stream; it takes place mainly in the months of June and July and is at its maximum in early July, although it tends to be somewhat earlier in the lower zones than in those further upstream. The wide-spread distribution of the spawning is further illustrated by Fig. 4, which shows the distribution of the redds in each section of the stream.

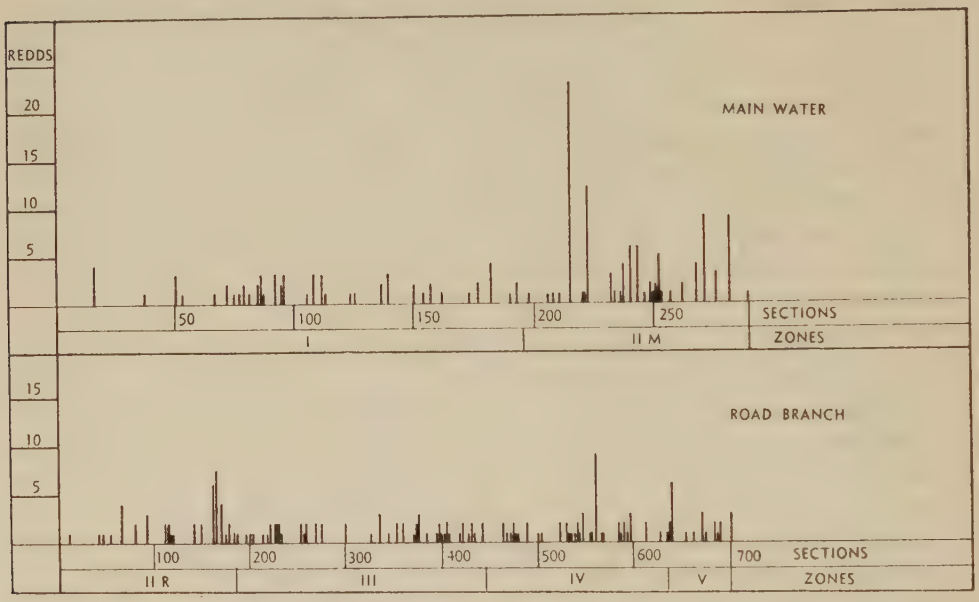

FIGURE 4. The distribution, by sections, of the observed redds in the Main Water and Road Branch in the 1940 spawning season.

The completeness of the record of redds may be checked by comparing the number of redds with the estimated egg production. If the estimated egg production of 888,550 were contained in the 356 redds recorded, the average redd would contain 2,500 eggs, the means for the zones ranging between 687 in Zone II R, and 3,645 in Zone III. Insufficient redds were excavated to give a direct estimate of the mean egg content of the redds in the Horokiwi. An indication as to the probable value can, however, be found in the work of Hobbs (1940) who excavated a large number of brown and rainbow trout redds in various parts of New Zealand. The mean content of the 541 redds examined was 791 eggs, and there was relatively little variation between different districts. In most of the waters examined spawning fish were usually larger than in the Horokiwi, and consequently the average egg content could have been expected to be rather greater than in the Horokiwi. The egg content calculated from the estimates of egg production and the redd counts therefore seems to be three to four times the probable value. Such a large discrepancy could arise from a number of causes, including failure of eggs to lodge in the redds, or a low estimate of the number of redds formed, or a high estimate of egg production. Previous discussion has shown that the main source of probable error in the egg production estimate lies in the estimate of the size of the total population. A high estimate of egg production would therefore probably

be due to a high estimate of total population. Hobbs (1940) has shown that lodgment is probably reasonably complete. It seems therefore most probable that the discrepancy arises from inaccuracies in either the redd counts or the population estimates; this probability is increased by the further discrepancy between the estimated number of mature females and the number of redds recorded. Table 32 shows that the estimated total number of mature females spawning in 1940 was 989, while the number of redds recorded was 356. The studies of previous workers (Greeley, 1932, Hobbs, 1937, Jones & King, 1949) have indicated that female salmonid fishes generally form several redds in each spawning season. The deficiency in the number of redds recorded is therefore at least as great when compared directly with the estimated number of spawning females as when compared through the medium of estimated total egg content. In view of this and of the direct evidence of other workers to the contrary, there appears no reason to ascribe any significant part of the deficiency to failure of eggs to lodge in the redds. It has been shown above that there is a 95 per cent. probability that the estimates of the trout population are correct to within about $\pm$ 50 per cent. The discrepancy between the number of redds observed and the number which the estimated population of females would have formed is much greater than this, and the conclusion appears to be inevitable that despite the careful and frequent observations a considerable number of redds were not recorded. Further evidence of this is provided by the fact that the estimated number of fry in each zone in 1941 is much less closely correlated with the number of redds observed ($r = 0.36$), than with the estimated egg production from the mature females in the same zone ($r = 0.76$). There were probably also appreciable differences between the various zones in the completeness with which the redds were recorded. The records seem to have been most complete in Zones II R and V, where the number obtained by dividing the estimated egg production by the number of recorded redds is not greatly in excess of the probable egg content, and where the number of redds recorded was greater than the estimated number of mature females. In Zone I the number of fry estimated to be present in January, 1941 is high in relation both to the number of redds and to the number of mature females; this suggests that there may be some downstream migration to the lower reaches during the first three months of life. It should be noted that the estimate of the adult population used as a basis for the estimate of egg production in 1940 was made during July when spawning was at its height, and when fish might in consequence be expected to be found close to the places in which they actually spawned.

Part of the deficiency in the recording of redds may have arisen from the difficulty in determining how many redds had actually been formed where several fish had spawned in succession on the same patch of stream bed. Any change in the state of the surface between one visit and the next could generally be recognized so that the additional excavation was usually recorded, but one or more redds could be formed and then rendered unrecognizable by subsequent activity between one visit and the next. Where a single redd was covered by another single clearly defined redd this was unlikely, but where the later appearance showed traces of a number of redds, there was considerable probability that some redds which were no longer recognizable had been formed. Seven groups of such superimposing redds

were observed and, while 26 redds were recognizable in their final forms, 16 additional redds were known to have been buried in them. Eight other groups, also involving 26 redds, in which no known redds were subsequently buried, were observed. In 16 instances isolated redds were buried by another single redd superimposed upon them. In contrast, 241 single redds were identified and were not observed to be disturbed by subsequent spawning. Thus, although apparently only about one-third of the redds formed were recorded in 1940, the discrepancy seems likely to be due simply to failure to recognize redds rather than to their being hidden by later redds formed on top of them.

Only 35, or approximately 10 per cent., of all the redds seen were later so completely covered by other redds as to become unrecognizable. The proportion of these redds which were sufficiently disturbed for the eggs to be dislodged is not known, but it is quite possible for a redd to be hidden, particularly by the gravel from a redd slightly farther upstream, without the egg-pockets being re-excavated. The figure of 10 per cent. is therefore probably a high estimate of the proportion of eggs which were destroyed by later spawners working in the same area.

In 1940 the proportion of redds destroyed in other ways was also small. Only six redds, less than 2 per cent., were known to have suffered damage likely to lead to the destruction of the eggs. One of these was scoured out by a local movement of shingle during a fresh, but the others were accidentally destroyed by man. Four, in one short reach of stream, were left in still water, and subsequently silted up, when a local diversion of the stream was made. The other was destroyed when a farm tractor was frequently driven across the stream at the place where it had been formed.

In 1941 the wet weather and frequent floods not only made the location and recording of redds considerably more difficult than in the previous year, but also caused much damage to the redds themselves. In particular, the slight floods on 13th June and 10th July rendered a high proportion of redds unrecognizable. The data which were obtained have been combined with the information collected in 1940 regarding the rate of redd formation at different times, to give approximate estimates of the total number of observable redds which would have been formed in each zone. These estimates are shown, together with the numbers actually recorded, in Table 35. It is apparent that generally the totals are considerably greater than in the previous year. That this is not due to unsatisfactory methods of estimating is shown by the fact that the actual counts, known to be incomplete, are substantially greater in Zones II R, IV and V than they were in 1940. The Zone I and Zone II M counts are known to be very much more incomplete than those in the Road Branch zones. It is not possible to determine whether these increased counts are actually due to an increased spawning population or to improved ability to recognize redds, although Tables 32 and 33 show that there is reason to believe that the spawning population was actually higher in 1941. Despite this increase the estimate of average egg content of a redd would be 1,307 if the estimated number of redds were correct, and this is well above the highest probable figure.

The amount of damage to redds by floods will vary in any stream from year to year in response to the weather conditions prevailing during the critical months,

TABLE 35. The number of redds observed, the estimated total number of observable redds, and the estimated total egg production for each zone for the 1941 spawning season.

ZONE	No. OF REDDS. Observed.	Estimated.	Estimated Egg Production.
I	45	149	192,500
II M	31	103	309,700
II R	62	116	12,800
III	51	95	199,000
IV	81	152	139,450
V	34	63	32,800
Total	304	678	886,250

The years 1940 and 1941 in which redds in the Horokiwi were kept under observation represent almost the two extremes which had occurred during the years in which meteorological records had been kept in the district. In the dry year, 1940, only one of the 346 redds under observation was destroyed by a flood. In the very wet year, 1941, the stream bed was already unstable at the beginning of the spawning season as a result of the big flood in February, and consequently was disturbed very easily by the minor floods which occurred during the spawning season. Insufficient redds had been recorded prior to the flood of 13th June to enable an estimate to be made of the extent of the losses which it caused. Before the flood of 10th July 134 redds had however been recorded in areas which were examined again after the flood; of these, 102 (76 per cent.) could no longer be recognized. In some of these the surface of the redd would have been levelled off by the flood without disturbance of the eggs, but in others the disturbance would have been sufficiently deep to cause the destruction of the eggs. In only five cases, however, was the disturbance so extensive that the survival of the eggs was obviously improbable; one redd was left dry; one was obviously scoured out; and the other three were deeply buried under additional gravel.

The positions of a number of redds were carefully fixed at the end of June by triangulated measurements from pegs driven into the stream banks. Early in September all these sites were carefully examined, and unless the redd had obviously been destroyed it was carefully excavated so as to collect all eggs or alevins present. Thirteen redds were examined; two were in an area in the lower part of Zone II M where a long stretch of the channel had been artificially straightened; one was dry and yielded no eggs when excavated; two had obviously been so deeply scoured as to remove the eggs; the remaining eight were excavated. Of these only two yielded eggs or alevins, and the remainder had apparently been completely destroyed by the floods. Thus, out of eleven redds selected at random, nine (82 per cent.) had been destroyed by floods between the end of June and early September.

The last and one of the most severe of the floods of 1941 occurred on 2nd October. At this time the great majority of the ova would have hatched and the fry would be emerging from the gravel and beginning to feed. The young fry would however

be relatively vulnerable to floods whether they had reached the feeding stage, or whether they were still lying among the gravel as alevins. This flood must therefore have caused some losses in addition to those caused by the destruction of redds by the earlier floods.

(c) Mortality Rates

The data presented in the previous sections and set out in Table 30 provide a basis for the examination of the rates of mortality in the Horokiwi trout population. It is obvious from the figures that the absolute mortality rate is very much greater in the early part of the life of any year-class than it is later; in other words, that the actual number of fish dying from all causes in unit time decreases during the life of the year-class. Of greater significance, however, are the changes in the proportion of the population dying in unit time. These may be examined by plotting the logarithm of the population against time, as has been done for Zones I, II M and IV in Fig. 5. It is apparent that the relationship is approximately linear, so that the proportion of the population dying in unit time does not vary greatly. Deevey (1947) has described this type of relationship as a *diagonal survivorship curve*, as distinct from the *positively* and *negatively skew rectangular curves* in which the relative mortality rate is respectively much greater in the early stages or in later life, and has shown that it occurs in a number of vertebrates, particularly in birds. Ricker (1949b) has examined data collected by various workers from a number of unexploited fish populations, and has shown that in many populations this type of relationship occurred in later life; the data available did not as a rule yield any information regarding the earlier years.

Fig. 5 has been constructed by combining the successive population estimates of a number of year-classes and the results are therefore complicated by variations in their relative strengths. In fitting lines to these points, consideration has therefore to be given not merely to the over-all distribution, but particularly to the slopes indicated by the groups of points belonging to the same year-class. If this is done, there appear to be three successive stages with differing mortality characteristics; an early period of very high mortality, extending over about the first three months; a second period of relatively slight mortality of about one year; and a third period covering the remainder of life, when the mortality rate is rather greater than in the second period. The only population estimates available in the first period are those for the beginning and end, so that only an over-all average rate for this period can be determined. The population estimates for January, 1941, which is the junction of the first and second periods, are likely to be relatively lower than the other estimates; it is probable therefore that the transition between the mortality rates in the two periods is much less abrupt than the raw data indicate, although there seems no doubt that the rate is very much greater in the first few months than it is in the following year.

During the second period a number of points are available, and these suggest that the relative mortality rate remains fairly constant during this period. The relation between population and time may therefore be represented with reasonable accuracy by the expression: $N = N_0 e^{-mt}$, where N = population after time t, and N_0 is the original population and m the instantaneous mortality rate. Since

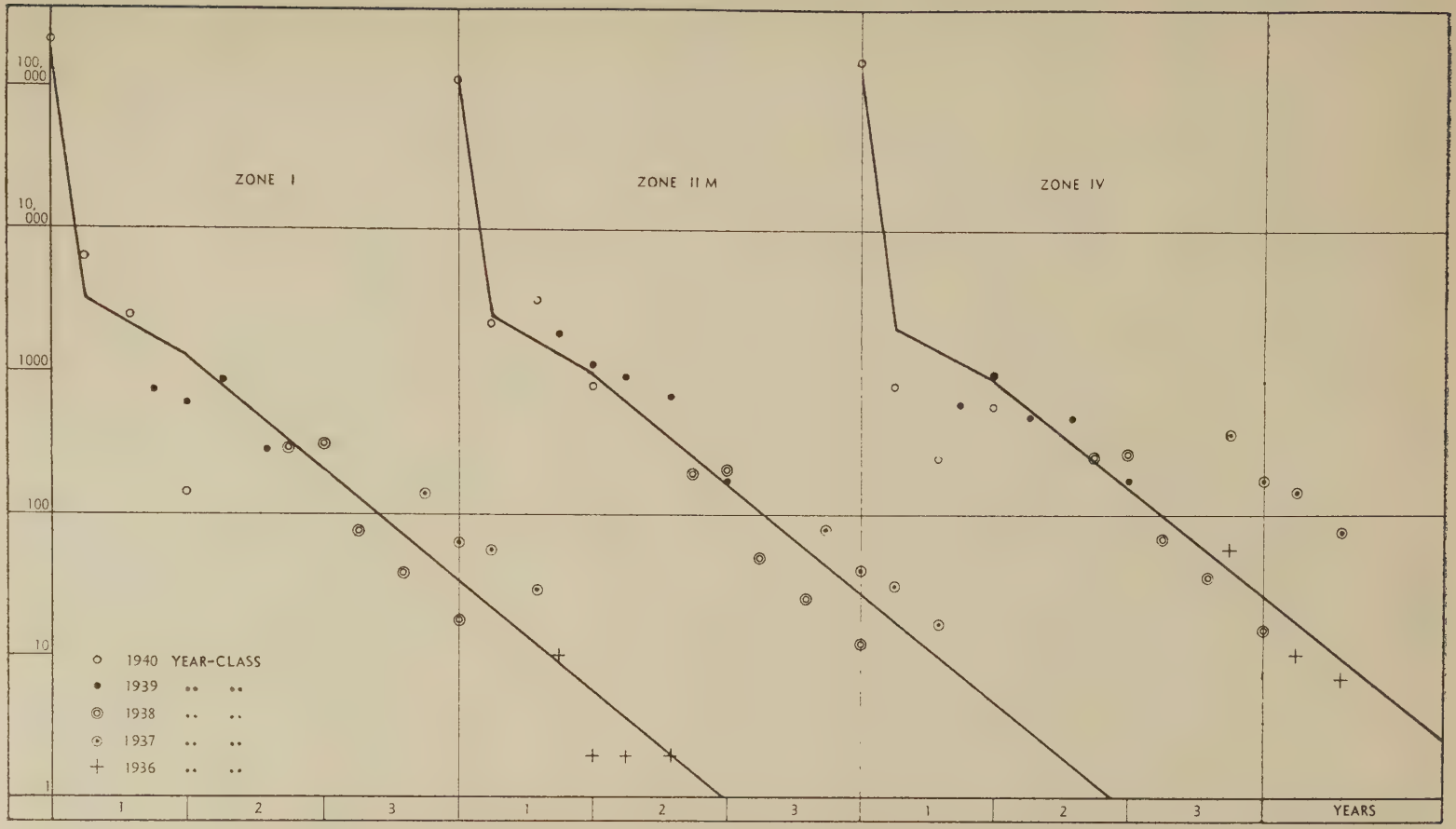

FIGURE 5. The estimated number of fish surviving to each age in zones I, IIM and IV, the data being taken from Table 30. The points for successive year-classes have been combined to represent a composite year-class in each zone. The vertical scale for number of fish is logarithmic.

the slope of the line corresponds to a survival over a full year of 28 per cent. of the initial population the value of m is 0.00349 if t is given in days.

In the remainder of the life of the year-class the slope of the line is appreciably steeper, and the average survival over a full year is about 17 per cent. of the initial population; the corresponding value of m is now 0.00486. In view of the wide limits of accuracy of the data, and the comparatively small degree of difference in the slopes for the second and third periods, it does not seem necessary to give any special consideration to the transition. It may be significant that the increase in the mortality rate is approximately simultaneous with the first spawning period and also with the beginning of exploitation by anglers.

The mortality rates found in the Horokiwi may be compared with those reported by Ricker (1949b) for the unexploited fish populations referred to above. In these populations, none of which consisted of trout, and which were all of relatively long-lived species, Ricker found that the annual survival rate, S, varied between 0.21 and 0.92, the corresponding values of m as used in this paper being 0.0046 and 0.0006. Thus the maximum mortality rate in these unexploited populations was very close to that found among the older Horokiwi trout, but the most usual values were well below this. A more relevant comparison is provided by the data of Schuck (1945) who studied a stream-living brown trout population, in which the survival from year to year over the first five years varied irregularly between 22 per cent. and 50 per cent. The corresponding value of m in this population, which was subject to angling, ranged between 0.0041 and 0.0019, with a mean of 0.0028. These mortality rates are thus similar to, but slightly less than, those found in the Horokiwi. The irregular variations may be due to sampling effects in a population which is actually subject to a steady mortality rate throughout its observed life. The first observations made by Schuck are in the autumn of the first year, so that no data are available regarding the mortality rates during the first few months.

Other data regarding mortality rates in trout populations in streams are provided by Shetter and Hazzard (1939); in two Michigan trout streams they found that the survival from year to year over the first four years varied irregularly between 14 per cent. and 35 per cent., with a mean of 20 per cent. This mean value corresponds to a daily value of m of 0.0044, which is very similar to the Horokiwi values. Needham, Moffett and Slater (1945) found that in Convict Creek in California the average survival of brown trout for one year after the first autumn averaged 15 per cent., although it varied from year to year between 9 per cent. and 41 per cent. being largely dependent on the severity of the winter; older trout apparently had rather higher mortality rates. The mean value in this case is equivalent to a value of m of 0.0052 which is apparently slightly higher than the normal Horokiwi values.

Changes in the rate of mortality during the early life of a salmonid fish have also been examined by Ricker and Foerster (1948), who have shown that during the fresh-water life of young sockeye salmon the instantaneous mortality rate falls steadily throughout the first year, rises abruptly in the following spring, and then again falls steadily. When converted to daily instantaneous rates, m, the means

over the first and second years are respectively 0.0077 and 0.0063, while the initial peak value is as high as 0.034. The annual mean values are very much of the same order as those found in the Horokiwi trout.

6. GROWTH AND CONDITION

(a) Growth in Length

Any population of animals may be assessed either numerically, as consisting of so many individuals which may be subdivided into types based on such considerations as sex and age; or else gravimetrically, as consisting of such a total weight of the species in the area, again possibly subdivided. In studies of production the gravimetric approach is generally essential, since the size of the individuals is a vitally important factor in considering such relations as utilization of food supply and yield to predators. On this basis production is derived both from reproduction and from the growth of individuals, and in most fish, where the size of the first feeding stages is very small compared to the adult, growth is much the more significant contributor.

Detailed study of the rate of growth of the trout of the Horokiwi therefore formed an important part of the present investigation. Growth may be expressed conveniently either as growth in length or as growth in weight. While the latter method is more directly applicable to productivity investigations, growth in length is more easily studied by indirect means, and consequently there is a great deal more material of this type available for comparison. For this reason, and because both kinds of data were equally available, the studies of the growth of the Horokiwi trout have been based on both length and weight. It is unfortunate that the length of a fish can be expressed in so many different ways: the three basic forms of length measurement are the total over-all length, the fork length from the tip of the jaws to the fork of the tail, and the standard length. Minor variations of these have been used by various workers, and Ricker and Merriman (1945) list no fewer than eleven different measurements of length which have been recorded. Fork length seems to be the most convenient when considerable numbers of fish have to be handled in the field, and it has accordingly been used in this work.

The methods available for the study of the growth of wild fish fall into three main categories. The first of these is based upon the study of the size of individuals of known age. If adequate samples can be obtained at fairly frequent intervals good data regarding the average growth and the usual range within the population can be obtained in this way. The method may, however, be subject to systematic errors which can arise from various causes, and particularly from population movements; it is also dependent on the accurate determination of the age of the individuals measured or weighed. A more direct approach is provided by marking and releasing fish which are subsequently recaptured after varying intervals. This method depends on the assumption that handling and marking fish does not cause their growth to deviate significantly from the normal for the population; it may also suffer from sampling errors due to difficulty in obtaining an adequate number of recaptures. If the results are to be fully interpreted, other methods have to be used to determine the age of the fish at the first marking.

The remaining and probably the most widely used method is based on the back calculation of the lengths of individual fish at earlier dates in their lives from the traces left by seasonal growth on their scales and other structures. This method is subject to inherent complications caused both by the difficulty in identifying with absolute certainty the dates corresponding to particular appearances on the scale, and by the variable and sometimes complex nature of the relation between the length of the scale and the length of the fish. These complications have been examined in particular instances by a number of authors, and have been generally reviewed by Van Oosten (1941) and Carlander (1950). The method has also the disadvantage that it is rarely possible to identify and calculate sizes for more than one point in each year of the life of the fish. This makes it particularly unsuitable for use in studies of production where more detailed growth curves are generally desirable.

The most suitable method for the present investigation therefore appeared to be that first described, i.e., the measurement from time to time of samples of known age. All that is needed for this purpose is the collection and measurement at suitable intervals of adequate numbers of fish, and the development of some means of determining the age-group to which each fish belongs. In most species of fish, the 0 age-group can be distinguished during at least the first few months simply by size, since there is normally a gap in the size range between this and older age-groups. The length of the period during which this method of age-determination may be used effectively depends upon the relation between the rate of growth and the amount of individual variation in the population. In the Horokiwi it was found that the rapid rate of growth, and the high degree of uniformity which occurred in any one part of the stream made this method available for an unusually long period. It was normally possible to determine the age of fish on the basis of size alone up to the end of the second year of life; beyond this point ages were checked by the examination of scales, and a very few younger fish of intermediate sizes were also checked in this way. The large number of scale samples of fish of known age up to two years which were available for comparison made it possible to reach a high degree of certainty in the determination of age from scales; only one fish whose age could not be satisfactorily assessed was encountered in the entire collection.

The main bulk of the material for the growth studies was obtained by measuring every fish caught in the quarterly routine collections. Smaller samples were also obtained from the collections made at monthly intervals for the examination of stomach contents, and from special collections made at more frequent intervals during the first few months of life of each year-class.

It became apparent very early in the work that the normal growth rate varied very substantially in different parts of the stream, and that it would consequently not be possible to establish a single standard growth curve which could be used

TABLE 36. The actual and corrected mean lengths of fish of the 1939 year-class taken in the routine nettings between July, 1940, and April-June, 1941.

NETTING STATION.	JULY, 1940.			OCTOBER, 1940.			JANUARY, 1941.			APRIL–JUNE, 1941.		
	No.	Actual Mean (cm.).	Corr. Mean (cm.).	No.	Actual Mean (cm.).	Corr. Mean (cm.).	No.	Actual Mean (cm).	Corr. Mean (cm.).	No.	Actual Mean (cm.).	Corr. Mean (cm.)
MA	..	..	..	..	..	..	..	..	..	5	31·24	31·66
MB	..	..	..	..	..	..	..	..	..	2	29·00	29·40
MC (M II)	12	20·53	20·78	..	..	..	14	29·07	29·36	4	32·60	32·88
MD	..	..	..	..	..	..	..	..	..	6	32·97	33·23
ME	..	..	..	..	..	..	..	..	..	4	32·80	33·00
MF	..	..	..	..	..	..	..	..	..	12	27·48	27·65
MG (M IV)	40	20·11	20·18	21	24·47	24·07	14	26·45	26·19	..	..	..
MH	..	..	..	..	..	..	..	..	..	24	27·87	27·96
MI (M V)	21	18·55	18·57	14	22·59	22·35	14	25·64	25·48	17	27·89	27·94
RA	..	..	..	..	..	..	..	..	..	8	28·35	28·35
RB	..	..	..	..	..	..	..	..	..	3	28·07	28·03
RC (R II)	4	17·58	17·65	3	20·10	20·20	2	24·80	24·82	5	25·10	25·02
RD	..	..	..	..	..	..	..	..	..	11	26·22	26·12
RE	..	..	..	..	..	..	..	..	..	29	23·98	23·85
RF	..	..	..	..	..	..	..	..	..	22	23·12	22·94
RG (R IV)	16	14·70	14·85	25	18·04	18·23	13	21·68	21·67	14	23·93	23·72
RH (R V)	15	17·78	17·99	18	20·04	20·34	10	22·37	22·51	10	26·89	26·64

TABLE 37. The actual and corrected mean lengths of fish of the 1940 year-class taken in the routine nettings of January, 1941, and April-June, 1941.

NETTING STATION	JANUARY, 1941.			APRIL–JUNE 1941.		
	No.	Actual Mean (cm.).	Corr. Mean (c.m).	No	Actual Mean (cm.).	Corr. Mean (cm.)
MA	..	..	..	12	15·28	16·40
MB	..	..	..	23	15·89	16·95
MC (M II)	70	9·85	10·50	42	16·59	17·41
MD	..	..	..	52	16·55	17·25
ME	..	..	..	49	17·22	17·76
MF	..	..	..	50	16·04	16·50
MG (M IV)	36	11·51	10·96	34	15·66	15·98
MH	..	..	..	98	15·63	15·87
MI (M V)	33	10·09	9·77	61	15·83	15·90
RA	..	..	..	45	16·07	16·07
RB	..	..	..	5	15·78	15·66
RC (R II)	11	8·78	8·84	5	15·62	15·35
RD	..	..	..	20	14·85	14·54
RE	..	..	..	24	15·50	15·05
RF	..	..	..	6	14·60	14·08
RG (R IV)	20	8·58	8·55	12	13·78	13·15
RH (R V)	11	8·43	8·79	18	15·55	14·79

to develop production statistics over the whole stream. The best data regarding the distribution of growth rate are those derived from the routine nettings carried out in July and October, 1940, and in January, 1941, and the large scale netting between April and June, 1941. The results obtained in this way for the 1939 and 1940 year-classes are shown in Tables 36 and 37, and Fig. 6. Since the netting operations, particularly of April–June, 1941, extended over a fairly long period and the fish were then growing relatively fast, direct comparison of the average lengths as recorded would be unsound, because the fish taken towards the end of the period would have been growing for a longer time than those taken earlier.

To minimize this effect, the corrected lengths shown in the tables have been obtained by reducing all the results for each period to a single mean date, by using the approximate average rate of growth from the growth curves. In the April–June data, where this effect is most significant, the mean date selected was 20th May, and the correction rates used were: 1939 year-class, Main Water—0.015 cm./day, Road Branch—0.010 cm./day; 1940 year-class, Main Water—0.04 cm./day, Road Branch—0.03 cm/day.

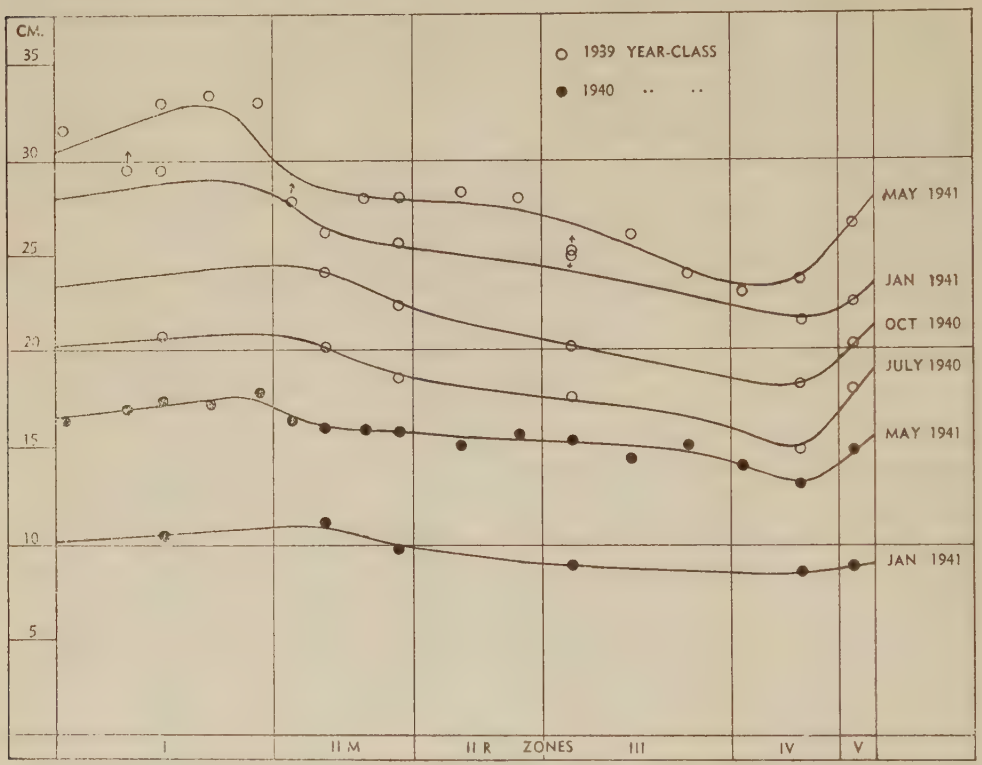

FIGURE 6. The distribution along the stream of the mean length of the 1939 and 1940 year-classes on a number of dates.

A fairly consistent pattern for the distribution of growth rate emerges from these results in all the periods examined. Growth is most rapid in the lower half of the Main Water and then decreases somewhat abruptly at a point about half-way up the Main Water; above this point it is fairly constant in the rest of the Main Water and in the lowest part of the Road Branch; farther upstream, at about station R B, the growth rate again decreases; it reaches its minimum level at about stations R F and R G; and finally increases again at the top of the observed area in station R H. From these results, it seems possible to distinguish five zones in the Horokiwi, each with a characteristic and fairly uniform growth rate. The rate of growth falls progressively upstream through the first four zones, but rises again in the fifth and highest zone. These zones are set out in detail in Table 6, and it appears that they correspond to regions of the stream with distinct physical characteristics. The exact boundary lines between the zones were based on the

physical features of the stream, but it is evident from Fig. 6, where they are superimposed on the growth distribution curves, that they are not at all incompatible with the growth phenomena.

The division of the stream into this series of zones greatly simplifies subsequent analysis. It has already been used as a basis for summarizing the physical features of the stream, and the density and composition of the bottom fauna, and the distribution of the trout population. It can now be used as a basis for analysis of the results of the growth studies. Some such procedure is essential because, particularly in the early part of the work, the localities from which fish were collected for measurement were not fully standardized. Even after a standard collection procedure had been adopted, it was sometimes desirable to take fish for the examination of stomach contents from points just outside the routine stations in order to avoid undue local depletion of the population. The main data regarding growth were obtained from the 1939 and 1940 year-classes, since these were the dominant components of the population during the time of the investigation. From these two year-classes 150 and 77 collections were obtained, containing respectively 948 and 1,239 fish. The results are summarized in Tables 38 and 39.

TABLE 38. The mean size and condition factor, and mean date of capture, of fish of the 1939 year-class, grouped into zones and generally into months.

Zone.	Mean Date.	No. of Fish.	Mean Length (cm.).	Mean Weight (gm.).	Mean Condition Factor.
I	28/9/39	1	2·50	0·18	..
	2/11/39	5	3·88	0·84	..
	13/11/39	13	4·62	1·44	..
	23/11/39	13	5·20	2·31	..
	10/1/40	6	9·38	13·08	..
	9/2/40	3	9·93	15·00	..
	5/3/40	3	10·67	19·50	..
	3/4/40	3	14·70	48·83	..
	29/4/40	8	16·06	61·7	..
	21/5/40	3	18·53	82·0	126
	8/6/40	9	18·34	79·2	128
	28/7/40	12	20·53	104·8	120
	24/8/40	12	22·91	151·3	125
	30/9/40	7	22·93	150·3	123
	28/11/40	6	27·79	274·1	123
	19/12/40	4	27·82	299·2	133
	16/1/41	14	29·07	334·1	133
	17/3/41	4	30·25	343·0	123
	30/4/41	21	32·08	386·7	114
	3/7/41	3	32·80	402·3	113
	20/9/41	4	31·42	369·2	113
II	1/5/40	11	16·53	67·9	..
	16/5/40	63	17·33	66·3	125
	6/6/40	10	17·89	71·1	122
	27/6/40	9	18·44	81·8	124
	24/7/40	62	19·49	86·3	120
	23/8/40	15	19·83	95·4	122

Zone.	Mean Date.	No. of Fish.	Mean Length (cm.).	Mean Weight (gm.).	Mean Condition Factor.
	28/9/40	16	22·54	141·9	122
	13/10/40	2	24·00	170·5	123
	29/10/40	35	23·72	174·1	130
	27/11/40	20	23·90	170·9	124
	21/12/40	12	25·27	220·6	136
	2/2/41	28	26·04	229·4	130
	25/2/41	16	26·88	239·4	122
	18/3/41	12	28·26	272·0	120
	8/5/41	13	27·58	248·2	118
	16/5/41	53	27·95	262·7	118
	28/6/41	6	28·42	264·3	113
	18/9/41	5	29·92	294·4	109
	28/10/41	4	29·55	279·7	108
III	21/11/39	1	5·20	2·20	..
	23/4/40	2	14·75	48·75	..
	14/5/40	2	13·45	31·00	125
	21/7/40	4	17·58	71·2	126
	28/9/40	4	20·50	111·2	129
	18/10/40	3	20·10	102·3	124
	29/11/40	5	21·82	127·0	122
	23/12/40	4	22·50	151·5	132
	25/1/41	2	24·80	198·5	127
	24/2/41	2	22·95	153·0	124
	28/3/41	2	23·60	162·0	122
	2/6/41	45	24·65	186·8	122
IV	13/11/39	11	4·09	0·93	..
	26/11/39	8	4·37	1·29	..
	8/1/40	10	6·76	5·16	..
	9/2/40	7	8·49	9·99	..
	24/2/40	8	10·68	18·46	..
	2/4/40	6	12·68	29·92	..
	26/6/40	1	16·60	59·0	129
	18/7/40	16	14·70	40·5	123
	28/9/40	7	18·55	90·1	131
	18/10/40	29	18·14	77·4	127
	28/11/40	4	18·58	83·5	129
	21/12/40	9	20·53	108·9	124
	26/1/41	13	21·18	120·2	124
	26/2/41	5	21·16	120·2	123
	21/3/41	6	22·28	143·0	123
	9/4/41	4	22·48	136·0	119
	8/6/41	36	23·43	155·6	120
	25/9/41	3	23·50	166·0	125
	22/10/41	3	24·07	163·0	116

Zone.	Mean Date.	No. of Fish.	Mean Length (cm.).	Mean Weight (gm.).	Mean Condition Factor.
V	2/11/39	6	3·75	0·71	..
	6/1/40	6	7·05	5·12	..
	23/2/40	4	10·12	16·72	..
	23/4/40	6	15·12	50·58	..
	14/5/40	4	15·58	49·5	126
	4/6/40	26	16·60	59·1	123
	27/6/40	1	18·50	83·0	131
	16/7/40	15	17·78	69·5	119
	26/9/40	7	19·26	96·3	130
	13/10/40	22	20·31	110·4	128
	3/11/40	6	21·28	125·2	126
	27/11/40	6	22·70	146·0	122
	21/12/40	6	23·40	166·8	128
	20/1/41	10	22·37	149·9	134
	26/2/41	5	24·82	193·4	125
	19/3/41	7	25·03	191·6	122
	27/4/41	6	26·90	236·8	120
	14/6/41	10	26·89	241·0	123
	17/9/41	2	25·45	181·5	110
	21/10/41	3	26·27	219·0	119

TABLE 39. The mean size and condition factor, and mean date of capture, of fish of the 1940 year-class grouped into zones and generally into months.

Zone.	Mean Date.	No. of Fish.	Mean Length (cm.).	Mean Weight (gm.).	Mean Condition Factor.
I	6/10/40	17	2·72	..	..
	1/11/40	37	5·02	..	..
	26/11/40	26	6·52	..	..
	19/12/40	18	7·92	6·84	115
	16/1/41	70	9·85	13·63	129
	27/2/41	7	11·16	16·50	115
	17/3/41	12	13·43	30·92	122
	1/5/41	178	16·57	59·46	124
	3/7/41	4	18·22	70·7	126
	25/9/41	2	20·15	89·5	106
	3/11/41	1	21·2	113·0	118
II	7/10/40	42	3·08	..	..
	3/11/40	25	4·61	..	..
	27/11/40	33	6·23	..	..
	20/12/40	62	7·80	7·47	127
	2/2/41	69	10·83	17·56	128
	25/2/41	28	12·65	25·84	119
	18/3/41	22	11·94	21·62	120
	9/5/41	88	15·84	50·09	122
	16/5/41	209	15·79	51·06	124
	5/7/41	14	16·66	58·0	124
	18/9/41	8	18·90	75·7	116
	28/10/41	5	18·76	75·8	114

Zone.	Mean Date.	No. of Fish.	Mean Length (cm.).	Mean Weight (gm.).	Mean Condition Factor.
III	4/11/40	4	3·52	..	..
	1/12/40	8	5·59	..	..
	23/12/40	5	6·74	3·60	113
	25/1/41	11	8·78	8·64	123
	24/2/41	3	10·63	15·33	121
	19/3/41	7	12·06	24·00	125
	7/4/41	7	12·06	22·00	122
	1/6/41	49	15·25	45·82	124
	3/7/41	1	13·40	28·0	126
	29/10/41	3	18·57	79·3	123
IV	7/10/40	9	2·62	..	..
	4/11/40	9	3·26	..	..
	22/12/40	15	6·49	3·60	122
	26/1/41	20	8·58	8·30	124
	26/2/41	1	11·70	20·5	128
	21/3/41	14	11·94	21·57	122
	9/4/41	5	11·66	20·20	125
	9/6/41	19	14·06	35·42	124
	25/9/41	2	14·85	39·00	117
	22/10/41	4	18·38	73·5	119
V	7/10/40	7	2·46	..	..
	4/11/40	3	3·30	..	..
	20/1/41	11	8·43	7·54	129
	26/2/41	3	10·73	14·83	120
	21/3/41	10	12·33	24·20	125
	25/4/41	6	15·00	41·00	121
	14/6/41	18	15·55	48·50	122
	17/9/41	4	18·52	78·7	123
	21/10/41	4	19·42	89·5	114

In these tables all results within each zone are combined, and the collections are also grouped on an approximately monthly basis, the mean date being shown for all the measurements made within each month. For the older year-classes, wider grouping for time is desirable on account of the small size of the samples, and the slower growth rate in later years of life makes it practicable. Grouping on a half-yearly basis has therefore been used for the 1938 and 1937 year-classes, and the results are shown in Tables 40 and 41. The numbers of collections and of fish measured for the year-classes 1938 and 1937 were respectively:—66 collections, 110 fish, and 52 collections, 83 fish. The numbers of fish measured in the earlier year-classes, 1936 to 1932, were respectively 16, 10, 5, 1, 1; the samples of these year-classes from the individual zones were too small to provide any reliable data, although the results are in accordance with those obtained from the larger year-classes.

TABLE 40. The mean size and condition factor, and mean date of capture, of fish of the 1938 year-class, grouped into zones and half-yearly periods.

Zone.	Mean Date.	No. of Fish.	Mean Length (cm.).	Mean Weight (gm.).	Mean Condition Factor.
I	3/5/40	5	31·32	372	121
	31/8/40	8	34·79	491	117
	12/3/41	4	37·10	613	123
II	23/5/40	13	29·50	313	122
	13/10/40	20	31·76	380	116
	16/4/41	8	33·61	430	117
	29/10/41	1	37·80	558	114
III	14/5/40	1	26·90	235	121
	26/9/40	9	28·34	275	118
	12/5/41	4	30·68	341	117
	1/11/41	1	30·90	353	119
IV	22/3/40	3	21·23	119	124
	8/10/40	17	24·33	163	113
	3/4/41	6	25·15	217	120
	25/9/41	1	26·80	205	106
V	6/10/40	7	27·47	258	116
	21/5/41	2	31·90	421	128
	18/10/41	1	35·50	477	106

TABLE 41. The mean size and condition factor, and mean date of capture, of fish of the 1937 year-class, grouped into zones and half-yearly periods.

Zone.	Mean Date.	No. of Fish.	Mean Length (cm.).	Mean Weight (gm.).	Mean Condition Factor.
I	28/9/39	2	37·00	590	115
	3/7/40	2	35·75	602	124
	6/3/41	6	42·05	882	118
II	25/5/40	4	32·30	399	116
	13/9/40	13	33·66	437	111
	1/4/41	4	37·72	636	115
III	23/4/40	1	28·50	290	125
	12/12/40	2	33·55	449	118
IV	22/3/40	9	26·99	233	118
	5/9/40	22	26·99	219	110
	13/2/41	3	25·90	207	118
	8/6/41	5	27·88	257	118
V	29/2/40	1	30·50	352	124
	17/10/40	6	32·48	401	112
	9/2/41	3	34·83	477	109

These results indicate that the growth rate distribution shown in Tables 36 and 37, and Fig. 6, is a normal characteristic of the Horokiwi trout population throughout life. The combined results for the 1936 to 1940 year-classes are shown graphically in Fig. 7 for Zones II and IV which provide the largest and best distributed samples.

It is of interest to compare the growth rates found in the various parts of the Horokiwi with those recorded from other waters in New Zealand and elsewhere in which brown trout populations have been studied. The first general studies of the growth of brown trout in New Zealand were made by Godby (1919) who used the scale method, then newly developed. Working on collections taken from

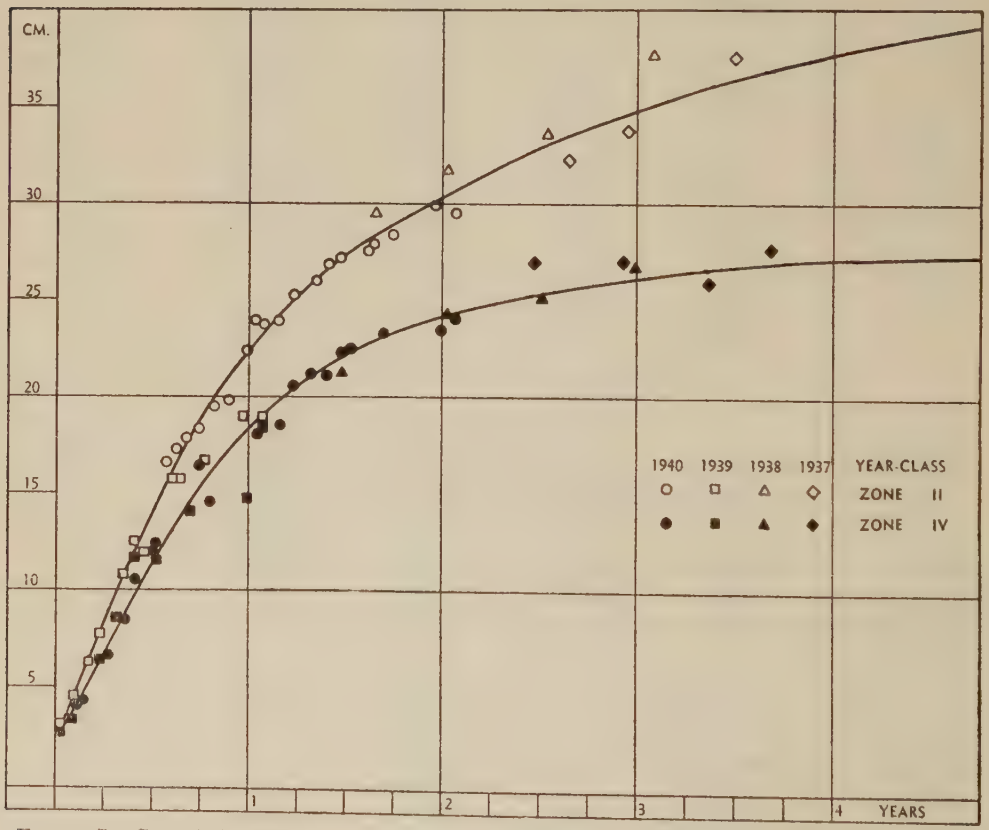

FIGURE 7. Growth in length of trout in Zones II and IV; combined results for the 1937 to 1940 year-classes.

a number of waters in the Canterbury district of the South Island, Godby found the growth rates in different waters were fairly consistent; the average lengths at the end of each of the first three years had the following ranges:—first year—11.2–14.0 cm.; second year—22.8–32.1 cm.; third year—30.5–43.7 cm.

Later Parrott (1932, 1934a, 1934b) described in a series of papers the growth of brown trout in a number of New Zealand waters. The waters studied were

PLATE IX (a). Netting a pool in Zone I; in this pool, where the current is relatively quiet, the seine has been laid round the lower end of the pool and is being worked up and will be beached in the shallow water at the head.

PLATE IX (b). Taking a square-foot sample of the bottom with the standard scoop; while the downstream operator guides the scoop and forces it into the stream-bed, the upstream operator pulls it forward for 12 inches.

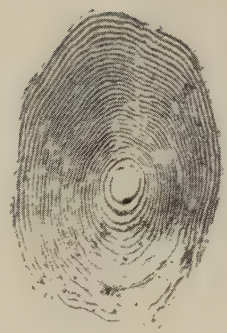

PLATE X (a). A typical scale from a Horokiwi trout at the end of its first summer, in this case a fish of 16.3 cm. taken in Zone I on 23rd April, 1941. The increase in the width of the circuli about two-thirds of the distance to the edge of the scale gives the appearance of summer growth following a winter-band, and it is suggested that this effect may have led some workers to determine the age of New Zealand trout as often being one year greater than was actually the case.

PLATE X (b). A scale from a trout caught in the lower waters during its second summer. This typical scale which is from a fish of 29.5 cm. taken in Zone I on 16th January, 1941, shows that no zone of narrow circuli was formed during the previous winter, when the fish would have been about 20 cm. long. A marked reduction in the width of the circuli has, however, occurred about the middle of the second summer.

PLATE X (c). A typical scale from a Zone IV fish of the same age as that on Plate X (b), in this case a fish of 21.8 cm. taken on 21st January, 1941. The first winter-band is clearly evident on most fish from this part of the stream. The narrowing of the circuli about the middle of the second summer is as evident in this scale as in that from the fish from Zone I.

again mostly in the Canterbury district, but included others from the Oreti river in Southland to the Hutt river in the southern part of the North Island. The ranges obtained for each of the first three years were:—first year—7.6–15.0 cm.; second year—17.1–26.9 cm.; third year—25.4–38.2 cm. These results are substantially in agreement with those of Godby, and it may be noted that the figures for the Hutt river—12.2, 22.8, 31.8 cm.—are very similar to those recorded by both workers for the Canterbury district.

These growth rates are however very different from those found in the Horokiwi. If the end of the year is taken in the Horokiwi as being 30th September, the average lengths reached at the end of each of the first three years appear from Fig. 7 to be:—Zone II—22.0, 31.0, 35.0 cm.; Zone IV—18.0, 24.5, 27.0 cm. Thus, even in those parts where growth is slowest, the length reached at the end of the first year is significantly greater than was found in any of the waters referred to above.

Such a difference could arise in two ways; either the Horokiwi does, for some reason, contain trout which grow abnormally fast, or else the difference is due to the different techniques used in the two groups of studies. It is unfortunate that the scale reading technique is so highly subjective that there can be no certainty that two independent workers will obtain the same results from the same collection of scales. This uncertainty becomes still greater if only one of the workers is aware of previous growth data applying to the population under consideration. For this reason it is not satisfactory to attempt to investigate the source of the differences by constructing growth curves based on the results of the examination of Horokiwi scales. It has however been mentioned above that the growth curves obtained by scale reading for the Hutt river were very similar to those obtained by this method from other waters. The Hutt river has a course parallel to the Horokiwi at a distance of only about six miles, and it is of the same general type although very much larger. The available information does not suggest that the trout stock in the Hutt is any more dense than in the Horokiwi, and the apparent difference in growth rate suggested by the data would therefore seem rather unlikely. When the figures for the two rivers are compared in more detail, it is noticeable that the estimated sizes of the Hutt fish are very similar to those found one year earlier in the lower waters of the Horokiwi. Comparison also shows that while the great majority of the growth curves shown by Godby and Parrott are more or less linear throughout the life of the fish, the growth rate in all parts of the Horokiwi shows a progressive decrease. These observations lead to the conclusion that the difference in the apparent growth rates may arise, at least in some cases, from the identification as a "winter-band" of a formation which was actually laid down on the scales at some time during the first summer. This would cause the age of the fish at any subsequent point to be read as one year more than it actually was. This suggestion is supported by the appearance of the scales of Horokiwi fish, since the width of the circuli often continues to increase all through the first summer, and there is frequently a point at which a fairly abrupt increase occurs, giving an appearance similar to the commencement of "summer growth" after a "winter-band." This effect is illustrated in Plate X (a), which shows a normal Horokiwi scale from a trout of 16.3 cm. taken in Zone I, in April of its first year. This situation cannot

be finally resolved without the comparison of the results of the two methods on the same water. It appears more reasonable however that the apparent differences should arise from a systematic error such as that suggested than that trout should grow very much more rapidly in the Horokiwi, which was selected as a typical small trout-stream, and shows no other signs of being outstandingly productive, than in any other water which has been studied in New Zealand. It must be emphasized that the growth of the Horokiwi trout was followed so closely during the first two years that it is impossible for a systematic error of a year to have occurred in these results.

There are however some data available which make a further comparison possible. Hobbs (in press) has published the results of a study of the growth during the first summer of the trout in a number of small streams in the Grey river system in Westland. Direct comparison is complicated by the fact that the fry hatch later in these streams than in the Horokiwi, so that they average only about 2 gm. at the end of December, while in the Horokiwi the mean weight was about 7 gm. at this time. Despite this late start, the mean weights in mid-April in the Westland streams range from 7.0 to 14.3 gm., while the means for the various zones in the Horokiwi at this time are generally between 12 and 15 gm. Further comparisons can be based upon material kindly made available to me by D. F. Hobbs; this consists of three collections of fish, apparently in their first year, collected on known dates in different South Island rivers. A collection of 57 fish taken in the Selwyn river in mid-February had a mean length of 10.2 cm.; reference to Fig. 7 shows that this is very similar to the size of Horokiwi fish at that date, despite the fact that the Selwyn was one of the main sources of the material examined by Godby and Parrott, and showed, by scale-reading methods, growth rates distinctly less than those found in the Horokiwi.

On the other hand, the other two collections, both of 16 fish, had average sizes well below those of fish even in Zone IV of the Horokiwi at the same date. The mean lengths of these samples were:—from the Ashburton river in Canterbury, 9.1 cm. on 21st April, and from the Silverstream in Otago, 7.2 cm. on 4th March. These comparisons appear to lead to the final conclusion that the rate of growth of trout in the Horokiwi in the first one or two years is probably higher than in many other New Zealand waters, but that many more direct studies of growth are needed to determine whether it is actually abnormally high.

Most of the published data from the northern hemisphere where the brown trout is indigenous suggest that in that region growth in the early years is much less rapid than in the Horokiwi. Alm (1939), who tabulated data from a number of localities in Sweden, Norway and Ireland, records the mean length at the end of the first year as ranging between 4.5 and 8.0 cm., and at the end of the second year between 7.3 and 18.0 cm. This is despite the fact that the waters studied include several in which the final size is very much greater than in the Horokiwi. Similar results have been found by Frost (1945) for other waters in Ireland, and for English lakes by Allen (1938). In North America Schuck (1945) found that the average length of brown trout in Crystal Creek in the Adirondack Mountains at the end of each of the first three years was 7.85, 14.45, and 19.20 cm. These figures are very similar to those referred to above from European waters.

The rate of growth can be studied even more directly by observing the growth of identifiable individuals, such as fish which have been measured, marked and released, and then subsequently recaptured. A number of such observations are available from the Horokiwi. Comparison of these results with those obtained by the measurement of samples is complicated by the very irregular distribution of the releases and recaptures. Comparison has therefore been based not on actual sizes or increments but on the linear rate of growth. Fig. 8 shows the mean rate of growth plotted against the mean date between the measurements for the 49 fish which were observed over periods of 75 days or more; for comparison is shown a curve for rate of growth against time which is derived from the standard curves shown in Fig. 7. It will be seen that there is a good measure of agreement between the two sets of observations. This not only supports the validity of the growth curves which have been based on the measurement of the samples, but also indicates that in general the fish have not been adversely affected by the tagging to a significant extent.

The nature of the length distribution of the trout within each year-class has been examined by plotting on probability paper the results for most of the samples of 50 or more specimens taken in one place on one or two consecutive days. The

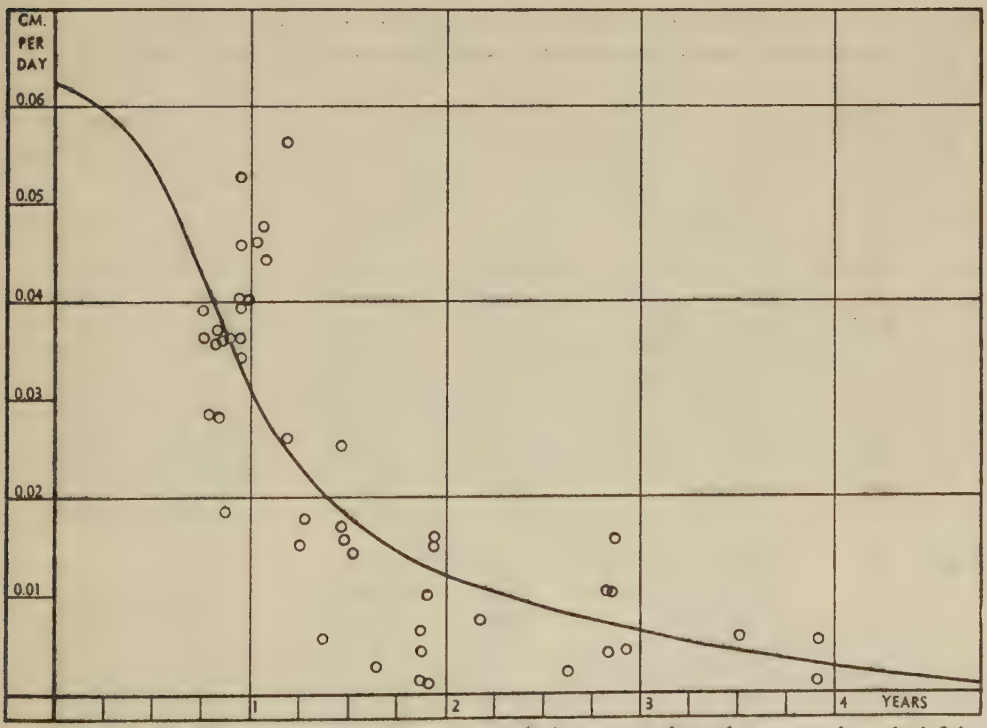

FIGURE 8. Comparison between the rate of growth, in cm. per day, of recaptured marked fish, and the mean rate of growth taken from Fig. 7.

resulting lines, which are all of the same form, indicate an essentially normal distribution, except that it is truncated at the upper end by about 3 per cent. With this type of distribution a reliable measure of the degree of spread is provided

by the standard or relative deviations. These have been determined for all collections of 16 or more fish of the 1939 or 1940 year-classes. The results are shown in Table 42; the relative deviation decreases steadily during the first year from an average value of about 0.185 to about 0.075, but subsequently it only decreases slightly. Since the spread is so small, the differences at any one time between the mean sizes of fish in the various zones are highly significant. For samples of 16 fish the probable range of the true population mean for 95 per cent. confidence decreases during the first year of life from about ± 10 per cent. to about ± 4 per cent. of the mean.

(b) Growth in Weight

As would be expected, the local distribution of growth in weight in different parts of the stream closely follows that of growth in length. The study of all aspects of growth can therefore be based on the division of the stream into the five zones described earlier. Tables 38 to 41 show the summarized data for the mean weights of each year-class in successive periods for each zone.

The nature of the weight distribution has been examined for the larger samples, and it appears to be generally more or less normal, although a slight degree of

TABLE 42. The mean and relative deviation (R.D.) in length (in cm.) and weight (in gm.) of each collection of sixteen or more fish taken in one place on one or two consecutive days.

YEAR-CLASS.	ZONE.	DATE.	LENGTH.		WEIGHT.	
			Mean.	R.D.	Mean.	R.D.
1939	II	14–15/5/40	17·4	0·086	67·0	0·258
	II	18–19/5/40	17·8	0·056	70·8	0·183
	IV	18–19/7/40	14·7	0·110	40·5	0·321
	II	23/7/40	18·5	0·080	76·2	0·233
	III	24–25/7/40	20·1	0·084	100·0	0·247
	V	12–13/10/40	20·0	0·094	104·9	0·273
	IV	15–16/10/40	18·0	0·076	75·8	0·238
	II	1/11/40	24·5	0·071	192·5	0·182
	II	13–14/5/41	27·8	0·075	261·4	0·231
	II	16/5/41	27·9	0·051	256·6	0·162
	III	2–3/6/41	24·0	0·065	173·1	0·196
	IV	6–7/6/41	23·1	0·061	151·1	0·183
1940	I	23–24/4/41	15·9	0·067	49·5	0·197
	I	30/4–1/5/41	16·6	0·099	60·6	0·261
	I	2–3/5/41	16·5	0·112	58·2	0·330
	I	6–7/5/41	17·2	0·099	67·7	0·293
	II	8–9/5/41	16·0	0·103	51·6	0·281
	II	12/5/41	15·7	0·110	49·1	0·316
	II	13–14/5/41	15·6	0·116	48·4	0·324
	II	16–17/5/41	15·8	0·111	51·5	0·336
	II	19–20/5/41	16·1	0·103	55·9	0·292
	III	30–31/5/41	14·8	0·115	42·5	0·363
	III	3–4/6/41	15·5	0·095	48·0	0·307
	V	14–15/6/41	15·5	0·131	48·5	0·361

negative kurtosis appears in some samples. The standard and relative deviations for all samples of 16 or more fish have been worked out and the results are given in Table 42. Since the weight is roughly proportional to the cube of the length, the relative deviation in weight should generally be about three times that in length, and similar changes should therefore occur in both measurements. Owing to the fact that the smaller fish had to be grouped for weighing in the field, relative deviations in weight are not available for the earlier samples, but it is clear that the trends are similar. The relative deviation in weight falls from about 0.3 in May of the first year to a steady value of about 0.2 in the second year. The length data suggest that earlier in the first year the value may be as high as 0.5. From this it follows that for samples of 16, the 95 per cent. confidence interval expressed as a percentage of the mean falls during the life of the year-class from about $\pm$ 27 per cent. to $\pm$ 11 per cent. In May of the first year, a period for which many observations are available, it would be about $\pm$ 16 per cent. Since, however, many samples are much greater than 16, and, at least during the first two years, the results of a large number of samples can often be combined, it is probable that the reliability of the smoothed values at any given date is normally considerably greater than this. The 95 per cent. confidence interval for the estimates of mean weight can probably be conservatively estimated at $\pm$ 5 per cent.

In many recent studies growth rates have been expressed in a logarithmic or "instantaneous" form, as the proportionate increase in the weight (or length) of a fish during a given time interval. This procedure has several advantages for analytical purposes; it greatly facilitates the combination of growth and mortality and exploitation rates for the study of production and cropping phenomena; it also simplifies the comparison between growth of fish under different conditions by eliminating one of the variables, the initial size of the fish.

Since the present study is concerned with production in the Horokiwi trout population, it is desirable to examine the instantaneous growth rate in relation both to local distribution and to variation with the age of the fish. The zones already described may be used to study the nature of the local distribution of instantaneous growth rate. The results are summarized in Table 43. This shows the mean instantaneous growth rate expressed as the mean daily increase in the natural logarithm of the weight, for each of the first two years in each zone. The rates have been computed as—

$$\frac{\log_e W_2 - \log_e W_1}{365}$$

where W_1 and W_2 are the mean weights at the beginning and end of the year. The starting weights in all zones have been taken to be 0.1 gm., which appears to be about the normal weight of trout fry at the commencement of active life. The weights at the end of the first and second years have been estimated from smoothed curves drawn from all the data given for the 1939 year-class in Table 38. The point of commencement of each year has been taken as 1st October, which is about the average date of emergence of fry in the Horokiwi. Two points arise clearly from this table. The first is that the well-marked differences in the size of

TABLE 43. The mean instantaneous growth rates of the 1939 year-class in each of the first two years in each zone.

Age-group.		Zone. I.	II.	III.	IV.	V.
O	Initial weight (gm.)	0·1	0·1	0·1	0·1	0·1
	Final weight (gm.)	165	125	95	70	100
	Growth-rate ..	0·0203	0·0195	0·0188	0·0180	0·0189
I	Initial weight (gm.)	165	125	95	70	100
	Final weight (gm.)	400	280	210	165	225
	Growth-rate ..	0·00242	0·00221	0·00217	0·00235	0·00223

adult fish in the different zones arise from differences in the instantaneous growth rates in the first year; the variations in the second year conform to no particular pattern and may be purely random effects. The second point is that the variations in mean growth rate between the two years are very large compared with the variations between the zones in either year alone. The change in growth rate during life is so pronounced as to make it desirable to examine the effect further.

For this purpose the instantaneous growth rate has been calculated between each successive pair of weight determinations in Tables 38 to 41. The central date of each interval has also been determined, and Table 44 shows for each month the mean value of the rate determinations which had their central dates within that month. Since the local variations were very small compared to the changes during the life of the fish, and the growth pattern was probably similar in all zones, the results for all zones are combined in Table 44. The table has been arranged in years of life rather than in calendar years in order to simplify comparison. In Fig. 9 the combined means for each month in the first year, and for each three-month period in the subsequent years, have been plotted against time. The result shows a very rapid drop during the first nine months to a minimum at about July of the first year; after this point the rate appears to rise slightly and then to remain

TABLE 44. The mean instantaneous growth rate ($\times 10^4$) in each month for each year of life. Results for all zones combined.

AGE-GROUP	O.		I.			II.			III.
YEAR-CLASS.	1940.	1939.	1940.	1939.	1938.	1939.	1938.	1937.	1937.
October	..	..	92	32	..	9	..	..	..
November	..	403	..	32	..	..	..	..	7
December	..	336	..	78	..	..	12	..	16
January	235	166	..	9	..	..	14	..	..
February	154	256	..	23	..	..	..	0	..
March	99	209	..	25	..	..	..	..	..
April	152	90	..	21	..	..	..	..	18
May	74	35	..	35	..	..	..	..	..
June	25	53	..	5	16	..	..	0	..
July	51	37	..	..	16	..	5	9	..
August	28	78	..	0	14	..	5	18	..
September	..	53	..	..	..	..	..	..	..

fairly constant during spring and early summer; after this time it again declines steadily. The apparent rise at the extreme end of the curve is probably only a chance effect due to the small numbers of fish upon which these points are based.

In its general form the curve, apart from the irregularities which are probably due to seasonal effects, appears to be a typical example of what has become known as a Minot curve, from the work of C. S. Minot (1891). Although Minot's method of computing growth rate has been criticized by a number of workers, who have pointed out the desirability of considering instead the continuously variable function

$$\frac{1}{W} \cdot \frac{dW}{dt},$$

the essential nature of the curve remains unchanged, and has been found to occur in the young stages of practically all animals investigated. Various attempts have been made to fit mathematical equations to the growth curves; the principal methods

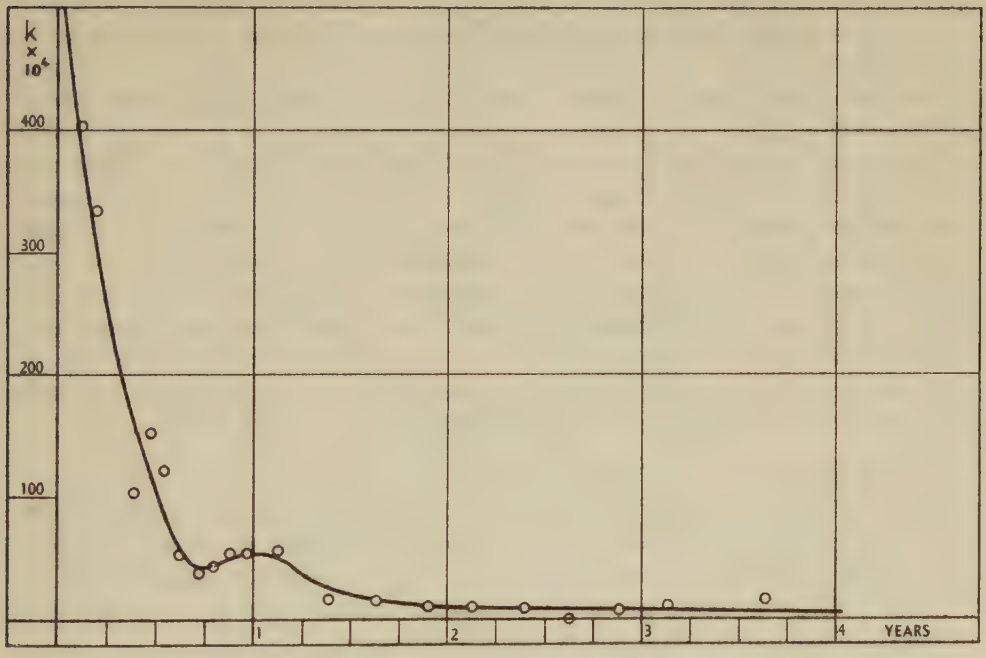

FIGURE 9. The mean instantaneous growth rate ($\times 10^4$) plotted against age of fish.

have been those of Brody (1927 and 1945) who has treated the growth curve as a succession of exponential curves so that the corresponding Minot curve becomes a series of steps; and of Schmalhausen (1926) and later workers who have developed equations of the general form—

$$\log W = k_0 + k_1 \log (t - n).$$

where W is the weight after time t from the commencement of development, n is the time up to the beginning of the period over which the equation applies,

and k_0 and k_1 are constants. These equations have generally been applied to embryonic growth and good fits have been obtained by selecting suitable values for n. The position with regard to salmonid fishes has been reviewed by Hayes and Armstrong (1943) and Hayes (1949) who consider that the second method is preferable, since it provides a single general description of the curve while weight measurements are generally too insensitive to provide a satisfactory test of the existence of discontinuities. Needham (1931) gives the value of k_1 for the embryonic development of trout as determined from the data of Kronfeld and Scheminzky as 2.06. Approximate values can be obtained from the data of Wood (1932) and these indicate that k_1 falls from about 5 at 12°C. to 1.5 at 3°C.

The post-larval growth of salmonid fish does not appear to have been analysed in this way, but the data of various workers suggest that the growth at this stage may also generally follow a Minot curve. Brown (1946) kept young brown trout under uniform conditions, and although irregularities occurred in the growth of individual fish it is evident that growth generally followed a Minot curve; the growth rate for the fastest growing fish fell from 0.037 to about 0.015 during the period of observations (32 weeks), and most of the fall occurred during the early part of this period. Since Brown's growth rates are given on a weekly basis, the above figures have been recalculated to bring them on to a daily basis for comparison with those given in Tables 43 and 44. Allen (1940) showed that a similar phenomenon occurred during each of the first two summers of growth of Atlantic salmon in the river Eden. These data were at the time interpreted as falling on a succession of exponential curves but they could equally well be fitted to smooth curves of the Minot type. The studies of Ricker and Foerster (1948) however gave rather different results. In this case the instantaneous growth rate for first year sockeye salmon in Cultus Lake, when converted to a daily basis, rose from about 0.008 to a maximum of 0.040 during May and June before descending in a sweeping curve to a zero value in the winter. It is not apparent from the data whether the early low growth rate is due to continued recruitment of newly hatched fish for a time, or whether these fish do actually grow relatively slowly at first.

On the other hand, some fish studied over shorter periods have shown growth which does not conform to the Minot curve. Thus, the data of Bonham (1950) show that fingerling rainbow trout (*S. gairdnerii*) under controlled conditions showed exponential growth over a period of 8 weeks. For these data the value of k in $W = W_o e^{kt}$ is 0.030, which is very similar to that shown by the brown trout of the Horokiwi during the middle of the first summer.

Since growth curves which conform generally to the Minot type seem to occur not infrequently in salmonid fish, it is of interest to examine how closely the Horokiwi data which also belong to this type can be fitted by the equation which has been fitted to embryonic growth data. In Fig. 10 the growth of the 1939 and 1940 year-classes in each zone has been plotted on double logarithmic scales, time being measured from 1st October in each year. It is evident that, apart from minor fluctuations, a fairly good fit to a straight line is obtained for the first 450 days in each zone. The slopes of lines fitted by eye show comparatively little variation, and, except in Zone I, probably do not vary significantly from a mean

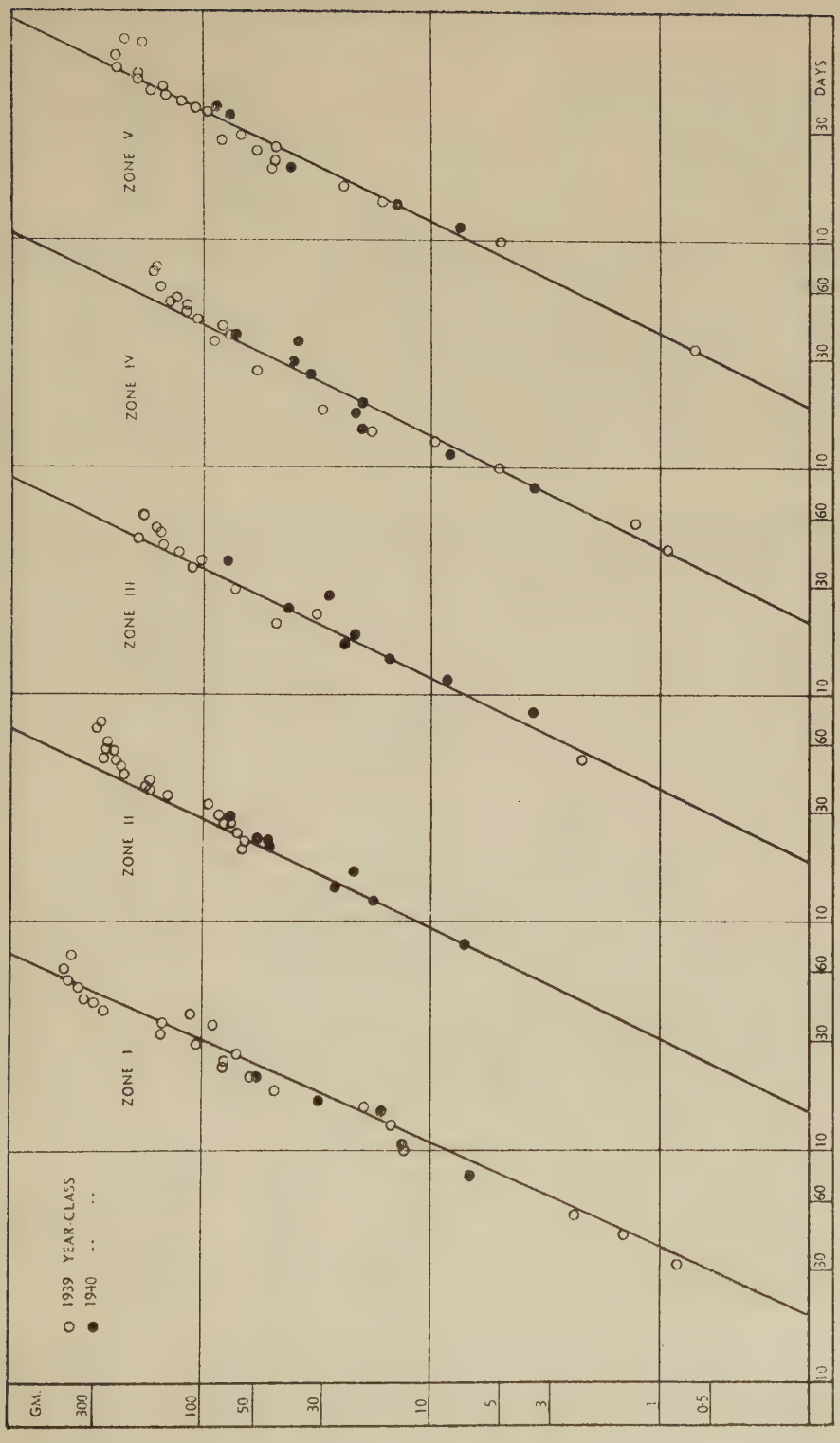

FIGURE 10. The growth of the 1939 and 1940 year-classes in each zone, weight being plotted against age on logarithmic scales. Age is counted from 1st October.

of 2.06. The constants for the lines shown in the figure are:

	k_0	k_1
ZONE I	0.00031	2.21
ZONE II	0.00087	2.06
ZONE III	0.00055	2.06
ZONE IV	0.00039	2.06
ZONE V	0.00052	2.06

The exact agreement between the most usual value of k_1 and that obtained from Kronfeld and Scheminzky's data for the embryonic stages is remarkable, but, particularly in view of the temperature effects which are known to occur, it would be unwise to attach too much significance to this result until more similar data are available. It has recently been shown by Burnet (in press) that growth of the Long-finned eel (*A. dieffenbachii*) also follows a curve of this type during much of the later part of its life. In this case the value of k_1 is very much higher, being 6.33.

Beyond 450 days it is apparent that the growth rate falls off more rapidly than the above formula provides. This change probably corresponds to the point of inflection of the usual sigmoid growth curve, and Brody, by applying the principle of mass-action to the upper section of the curve, has suggested it may be fitted by a line of the form—$W = A - B\,e^{-kt}$. It is not however unlikely that the decrease in growth rate in the trout of the Horokiwi is due not only to the inhibiting effect of the material already formed, as postulated by Brody, but also to changes associated with the onset of sexual maturity. The age at which the change in growth rate occurs corresponds closely with that at which development of the gonads first becomes clearly apparent. It is however of interest to endeavour to fit Brody's equation to the data available; this has been done by Brody's method which involves plotting log $(A - W)$ against t, and adjusting the value of A so as to obtain a linear relationship. This has been done for all zones, and the results for Zones II and IV are shown in Fig. 11. An approximately linear relation can be obtained, although the slope of the line cannot be determined with any high degree of accuracy owing to the spread in the later points resulting both from the nature of the logarithmic scale and from the small size of some of the samples. The slope also depends upon the precise value selected for A, which has to be chosen by a process of trial and error. The constants of the lines finally fitted to the various zones are:

	A	B	k
ZONE I	900	1190	0.00155
ZONE II	600	800	0.00158
ZONE III	500	630	0.00131
ZONE IV	270	377	0.00187
ZONE V	650	805	0.00115

Discussion up to this point has been concerned with the general trends of the growth curve rather than with the irregularities, although, as Hayes and Armstrong (1943) have pointed out, both have their significance. Part of the dispersal of the points about the lines which have been drawn in the various

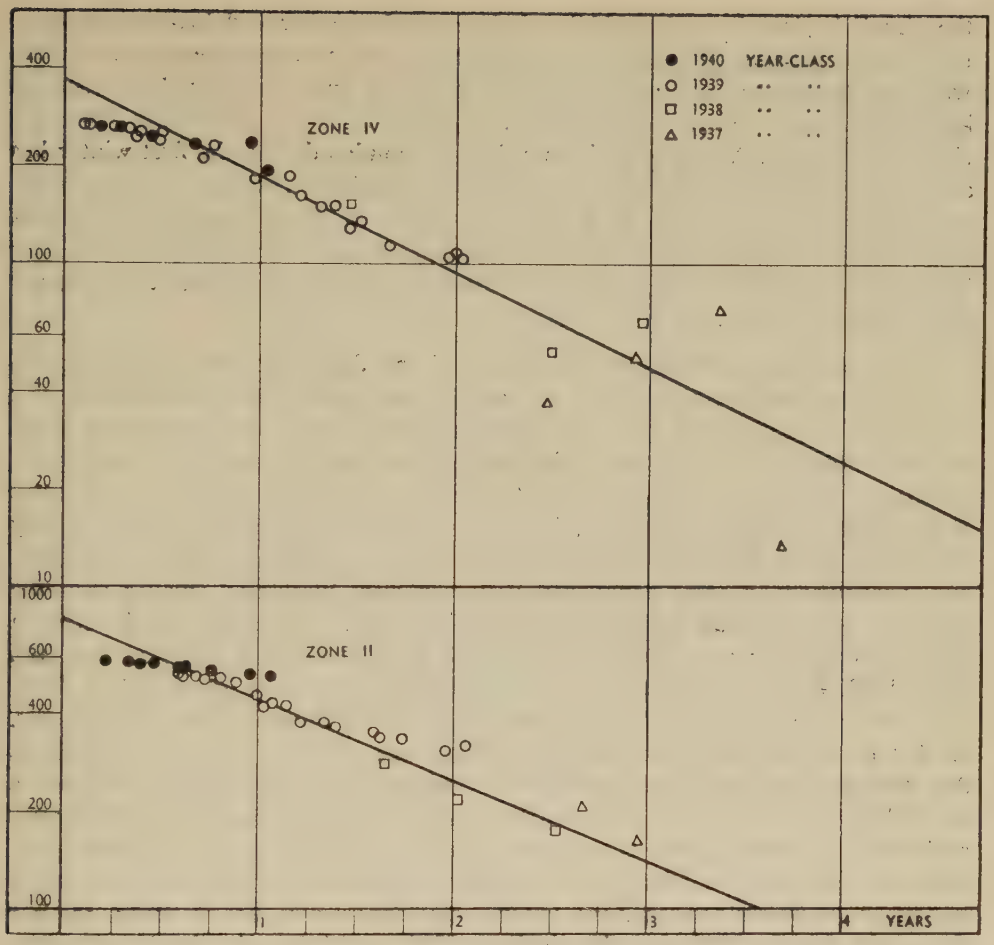

FIGURE 11. The value of $(A-W)$ plotted on a logarithmic scale against the age of the fish for Zones II and IV; the respective values of the constant A are 600 gm. and 270 gm.

graphs is clearly due to sampling effects, but certain definite trends are also discernible. The most important of these are the seasonal effects. The existence of the first winter check is clearly illustrated in Fig. 9 by the minimum instantaneous growth rate at about June. Examination of the data shows a tendency for the check to be greater in the upper part of the stream than in the lower part, and it is most pronounced in Zone IV. This result is supported by the appearance of the scales of fish taken from the different regions. In Zone I the great majority of scales show little or no trace of a winter-band, and the width of the circuli is almost constant from the first summer until well into the second summer. In Zone IV most scales show some degree of contraction of the circuli during the first winter, and, more distinctly, a sudden expansion in width in the following spring. Intermediate types and varying proportions of the extreme forms are found in the other zones. As a result it is possible to distinguish with a moderate degree of certainty between the scales of fish of like age taken in the different zones. It is also noticeable that in many scales from all parts of the stream a contraction of

the circuli begins about the middle of the second summer and becomes progressively more pronounced. It may be of significance that this occurs at about the time when the growth rate diverges from the Minot curve, and when sexual development begins to become evident. Typical scales showing the effects referred to above are shown in Plate X. A failure to form a distinct annulus during the first winter has also been described by Surber (1937) for Big Spring Creek in Virginia, where no annulus could be observed in 20–30 per cent. of the fish examined. In this case the lack of contraction in the width of circuli formed during the winter may have been due to lack of large seasonal variations in temperature, but this does not apply in the Horokiwi.

The growth data also show the effects of the floods of 1941. These caused serious disturbance of the stream bed and destruction of the bottom fauna. The reductions in the growth rate which occurred at this time are probably a result of these effects. The effect on fish in the first year may be seen by comparing the growth of the 1940 year-class in 1941 with that of the 1939 year-class in 1940. It is evident that up to February, 1941, the growth of the 1940 year-class closely followed that of its predecessors; after this time a divergence becomes apparent, and, particularly in some zones, the 1940 fish were noticeably smaller than the previous year-class had been at a corresponding age. This effect may be seen in Tables 38 and 39; a very direct comparison may be made in Zone II; on 16th May, 1940, the mean weight of the 1939 year-class was 66.3 gm.; on 16th May, 1941, the mean weight of the 1940 year-class was 51.1 gm., or only 77 per cent. of that of the previous year-class at the same age. Application of a t test shows this difference to be highly significant. A similar comparison, which also shows a marked decrease, can be made for Zone V in June. In the other zones direct comparisons at particular dates are not possible, but it is evident that the 1940 year-class were generally smaller than the 1939 year-class at the same age; the effect appears most pronounced in Zone II. It is also apparent in Fig. 7, where the last few points for the 1940 year-class in Zone II lie well below the line based on the older year-classes. The difference is much less pronounced in Zone IV. The same effect may also be seen in Fig. 10 where the final points for the 1940 year-class in Zones I and II dip noticeably below the line.

The same comparisons can be made for the next age-group by comparing the 1939 year-class in 1941 with fish of similar age in the previous years. The data for the 1938 year-class are insufficient to enable direct comparisons to be made, but Figs. 7 and 11 show that, in Zone II at least, the size of the fish of the 1938 year-class was well below the normal level in 1941. Most of the other zones show this effect to a less extent, but in Zone IV the 1938 fish were of normal size. It should be noted that in Fig. 11 the final points for Zone II swing above the line; this is because the vertical axis represents the amount by which the weight at any time falls short of a hypothetical maximum. The relatively large decrease in rate of growth in Zone II is in accordance with the view that this was an effect of the floods, since it has already been shown that the disturbance of the stream bed by the floods was greatest in this zone, and that, probably as a result, the greatest reduction in bottom fauna also occurred there.

(c) Length-Weight Relationship

The relationship between weight and length is not of direct significance to the problems of productivity. The work on growth has however involved the measuring and weighing of a large number of fish, and there is consequently a large quantity of data available regarding the length-weight relationship in the Horokiwi trout population. Since other aspects of the biology of this population are now known in a considerable amount of detail, it seems desirable that the data regarding this relationship should be briefly considered in relation to this background.

Study of the length-weight relationship in fish, and particularly in salmonid fish, has for many years been based on the "condition factor," which is generally determined as:—

$$K = \frac{AW}{L^3}$$

where A is an arbitrary constant selected so as to give a convenient result, and W and L are the weight and length of the fish respectively. Where the metric system is in use, A is generally made either 10^2 or 10^4 so as to give results which lie in the region of either 1.00 or 100. Provided that the density of the fish does not vary significantly, this relation implies that the condition factor will remain constant as long as the shape of the fish remains unchanged. It therefore tends to be a measure of changes in the fish, not only from season to season, but also over its whole life.

Recently various workers have incorporated the major trend of change in shape during life in the basic formula by using the form:—

$$K = \frac{AW}{L^n}$$

where n is a constant determined for the fish population under study, usually by measuring the slope of a straight line fitted to a plot of the data in the form log-weight against log-length. The value of n does not, as a rule, diverge greatly from 3.0. This method has the advantage that, by reducing the variation in K due to changes in form associated with growth, it gives additional emphasis to the short-term changes arising from seasonal and other similar effects.

In the present work it appeared that no great advantage would be obtained by making use of the generalized form, and the study of length-weight relationship has therefore been based on the usual condition factor, employing the cube of the length. The condition factor of all fish which were individually weighed and measured has been determined with a calculator of the Corbett type. As the metric system was used and A was given the value of 10^4, the condition factors were of the order of 100. The material obtained for the 1939 year-class before 3rd May, 1940, was not used for this purpose, since these fish were preserved in 4 per cent. formaldehyde for some time before weighing and measuring. This appears to have caused the condition factors to be rather too high, probably by producing a shrinkage in length. Since the length is cubed in determining condition factor, a slight error in length will have approximately three times the proportional

effect on condition factor. Shetter (1936) has shown that this shrinkage may amount to 5.5 per cent. of the original length, and this would increase the condition factor by 19 per cent. A few fish were found to have condition factors which were very widely divergent from the remainder of their group, so that a suspicion of incorrect measuring or weighing arose. Since the condition factor was found to have an approximately normal distribution, it was possible to check the actual occurrence of any degree of divergence against its theoretical frequency. It was found that the frequency of occurrence of divergences up to about 3.0 times the standard deviation was near the expected value, but that over 3.5 S.D. it was well in excess of the expectation, which is for only one in every 2222 cases. It was therefore decided to assume that all condition factors which diverged from the group mean by more than 3.5 S.D. were due to incorrect measurement and to neglect them.

Apart from the exceptions noted above, all condition factors are included in the results shown in Tables 38 to 41. The standard deviations of all samples of 16 or more fish were determined, and were found generally to lie between 5.0 and 7.5, the mean of 28 determinations being 6.09. No definite trend of variation of standard deviation with size or age was discernible. It is evident from the tables that there is a slight but definite downward trend in the condition factor as age increases; in the first year the values generally lie between 120 and 130, but afterwards they decline until they are usually between 110 and 120. There are not many indications of seasonal changes, but it is noticeable that in almost all zones there appears to be a peak about midsummer in the second year of the 1939 year-class. This may be associated with the more rapid growth which occurs at this time, after the first winter check and before the pre-spawning reduction in growth rate. It is peculiar however that the improvement in condition does not appear in Zone IV where the seasonal changes in growth rate appeared most pronounced.

It has already been shown that the floods of 1941 caused a decided decrease in rate of growth, and a similar effect is evident in the condition of the fish. Since it was Zone II which suffered most severely from the floods, it is not unexpected that the effects on condition are most conspicuous there. The effect appears in both the 1939 and 1940 year-classes. In the former year-class, the average condition factor fell sharply between 2nd February and 25th February from 129.8 to 122.3, and continued to decline during the rest of the autumn. By May it had fallen to 118.1, whereas in the previous year the condition factor of the 1938 year-class had averaged 124.1 at this time. In the 1940 year-class condition also fell sharply between 2nd February and 25th February, dropping from 127.6 to 119.0; there was some recovery after this but the mean value for May of 123.6 is still below that of the 1939 year-class which was 125.2. In the first three of these comparisons application of a t test shows that the probability of the differences arising from sampling effects is much less than 0.01, while in the last it is less than 0.1. It therefore seems certain that an exceptional fall in the condition of both the 1939 and 1940 year-classes occurred in 1941 in Zone II, and that most of this fall occurred during February, and followed the serious flood which then occurred.

If similar comparisons are made for other zones, it will be seen that a similar decrease occurred in every zone, but that it was not always as great as that in Zone II. The changes appear greater in Zones I and V, and less in Zones III and IV. The decrease in condition thus varied from point to point along the stream in much the same way as did the changes in rate of growth, the destruction of the bottom fauna, and the damage to the stream bed by the floods.

7. FOOD

(a) Methods

The food of brown trout in streams is generally derived from three main sources: the animals of the bottom fauna, the insects and other small terrestrial animals which fall into the stream, and the smaller fish. Data regarding the quantity and nature of the first and last of these sources of food in the Horokiwi have already been presented. A more direct approach may be made by examining the amount and kind of food actually eaten by the trout. The data for this purpose are derived from examination of the stomach contents of fish of all ages taken under a variety of conditions. The number of fish which could be examined was limited both by the time available and, particularly for the older fish, by the necessity of avoiding too much depletion of the population. In all 380 fish of 1939 year-class and 81 older fish were examined. Although these numbers are small, it will be shown that the consistency of the results obtained is sufficient to enable some definite conclusions to be drawn.

A number of methods have been employed for examining and recording the stomach contents of fish; the most usual and most accurate methods are either numerical, being based on the numbers of each organism present in each stomach, or gravimetric or volumetric, being based on the weight, or volume, of the stomach contents, either in total or by individual forms. A less informative but still relatively exact method is that based on the recording of the occurrence or absence of each organism in each stomach, regardless of quantity. A more approximate and subjective method is the "points" method of Swynnerton and Worthington (1940), in which numerical values are given to visual estimates, apparently by volume, of the amounts of the different animals present in each stomach. In a recent review, Hynes (1950), who used a modification of the "points" method in a study of the food of sticklebacks, has argued that it is preferable to the numerical and quantitative methods, not only on account of its relative speed and simplicity but also on account of the "spurious impression of accuracy" which the more exact methods are said to give. He maintains also that for similar reasons it is probably better to base faunistic studies on subjective impressions of the results of general sweeps with a dredge or net than on the counted or measured results of quantitative bottom samples. In this connection it is interesting to note that Macan (1949) who made a direct comparison of the two methods in weed beds found not only that the hand-net was not superior to the grab in taking scarce or widely spaced forms, but also that it was definitely selective in that it did not readily take some of the more active animals. While the "points" method may have an advantage where it is necessary to handle a large amount of material in the minimum amount

of time, it involves the description in an imprecise and subjective manner of the material which is actually handled rather than its objective measurement. In many cases the collection of material occupies a major part of the time available for an investigation, and once it has been collected it seems wasteful to fail to extract as much data from the material as is reasonably practicable. Errors due to failure to recognize or to separate partially digested or damaged food organisms must of course occur in numerical or other quantitative methods; but in many fish, including the salmonids, the food generally consists of a number of individual organisms of relatively large size, and these errors can therefore be kept to a reasonably low level by restricting investigation to the regions of the gut where comparatively little digestion has taken place. Under these circumstances the errors arising from damaged material will normally be small compared to the difference in accuracy between the best practicable count or measurement and a subjective estimate. Sampling errors are of great importance in almost all faunistic or food studies, but where properly quantitative data are available these can be determined by suitable statistical analysis so that the degree of accuracy of the results can be known. Where more descriptive methods are applied to the data, the numerical results may be similar, as Hynes points out, to those obtained from the same material by more precise methods, but their reliability, and hence their significance, cannot be assessed with similar confidence. Whatever the method by which the result is obtained, its greatest value lies in its interpretation, and in this interpretation due allowance must be made for the reliability and significance of the result; the more precisely the reliability is known, the more precise and the more valuable does the interpretation become. In order to obtain the greatest value from the original material it seems essential therefore to use methods which enable it to be described with the greatest practicable precision.

For this reason the methods used in the analysis of the stomach contents were made as accurate as was reasonably possible. Examination was restricted to the contents of the stomach itself, since further down the intestine digestion has proceeded too far to make identification and counting satisfactory. All organisms present were counted individually; in the case of disintegrated animals, the heads were counted since these are both most resistant and most universally distinctive. Identifications were normally taken to the same level as in the faunistic collections. For the gravimetric determinations, the contents of each stomach were dried at 65° C for three days before weighing as was done for the faunistic collections.

(b) Numerical Results

Since the bottom fauna, which is generally the most important of the three sources of trout food listed earlier, contains a great variety of forms in most streams, any effective study of the relation between fish production and food supply must make allowance for variations in the extent to which the different constituents of the bottom fauna are eaten by the fish. These allowances must be based on comparison between the composition of the bottom fauna and the composition of the stomach contents of fish feeding upon it. While relatively few such comparisons have been made, the earlier comparative data have been reviewed by Allen (1942) and some additional results have been brought forward by Leonard (1942).

Where comparable data are available for both fauna and food eaten it is necessary to develop means of performing the comparison so as to be able to correlate the results of different sets of observations. It has been suggested by the author (Allen, 1941a) and by Hess and Swartz (1941) that this comparison may be simply and usefully expressed by the ratio between the percentage of each organism in the stomach contents and its percentage in the fauna at the same time and place. This ratio, which was called the "availability factor" and the "forage ratio" respectively, does at least provide a measure of the relative extent to which the different animals are utilized as food. A more detailed discussion of the implications and limitations of the method has been given elsewhere (Allen, 1942). This method is however essentially a means of studying the relative degree of utilization of the different components of one only of the three main sources of trout food; it is necessary therefore to consider first the relative extent to which the trout of the Horokiwi derive their food from each of the three main sources.

The data on this point are summarized in Table 45. It is apparent that the bottom fauna is normally very much the most important source of food. Surface food is taken to some extent by fish of all ages, and shows some seasonal variation, being most abundant in the summer months. This is not unexpected since the forms taken most frequently at the surface are the adult stages of various insects, and the majority of these hatch during the summer. The only other terrestrial animals found at all frequently in the stomachs are a few spiders and millipedes. The adult insects include both purely terrestrial forms and the adult aerial stages of various types with aquatic larvae. The latter are much less abundant in the food than the terrestrial species, and only 73 (11 per cent.) of the 666 adult insects found in the stomachs had aquatic stages. In the limited amount of data available the insects of aquatic origin, notably Chironomidae and Ephemeroptera, were relatively more numerous in the stomachs of first-year fish than in the older fish. Since the fish examined were taken in all parts of the stream and more or less at random at all times of day between 9.00 a.m. and midnight, Table 45 probably gives a reasonably good indication of the proportion of surface food taken by trout in the Horokiwi. It appears that this is likely to be less than 5 per cent. by number of the total food intake when averaged over the year, although it may be somewhat greater for older fish than for fish in their first year.

TABLE 45. The percentage of food organisms taken at the surface or as small fish in the stomachs of trout caught in each three-month period of the investigation.

Year-class.		Oct.–Dec., 1939.	Jan.–Mar., 1940.	Apr.–June, 1940.	July–Sept., 1940.	Oct.–Dec., 1940.	Jan.–Mar., 1941.	Apr.–June, 1941.	July–Sept., 1941.	Oct.–Dec., 1941.
1939	Number of food organisms ..	485	1,120	1,133	4,645	7,925	3,851	1,187	1,163	274
	Percentage surface food ..	1·9	0·9	1·9	0·4	2·2	2·5	1·9	0·5	1·5
	Percentage fish	0	0	0	0	0	0	0	0·2	0
1938 and earlier	Number of food organisms ..	..	..	..	3,178	5,356	288	359	503	20
	Percentage surface food ..	..	..	..	0·5	6·5	4·5	2·9	0·2	0
	Percentage fish	..	..	..	0·2	0	0·7	0	0	0

The number of small fish in the food is evidently much smaller. Among all the fish examined only eight contained fish in any stage, and three of these each contained a single trout egg. Thus only five contained post-larval fish; of these,

three each contained a single *Gobiomorphus,* one a small *Anguilla,* and one had eaten two *Retropinna.* The youngest trout to contain a small fish was taken in September at the end of its second year. In all 91 trout of this age or older were examined, and only five (5.5 per cent.) of these contained small fish. These 91 trout contained a total of 10,254 organisms, so that on a purely numerical basis the quantity of fish in the food was negligible; since, however, the fish eaten were very much larger than the usual food animals of the bottom fauna, their significance is actually considerably greater than this. This point will be discussed further in a later section.

The bottom fauna is evidently the most important constituent of the food of trout in the Horokiwi, and further consideration must be given to the relative contributions which its different constituents make to the trout food. The composition and distribution of the bottom fauna have been examined in an earlier section of this paper, and it was shown that sixteen species or groups composed almost the entire fauna. As might be expected, these sixteen include all the principal sources of trout food, although there are noticeable differences in their relative proportions. The part of the food of the trout in the Horokiwi which is derived from the bottom fauna is dominated at all stages by five types in varying proportions; these are four Trichoptera larvae, *Helicopsyche, Olinga, Pycnocentrodes* and Sericostomatid type "C," and Ephemeroptera nymphs of the genus *Deleatidium*; the last group also includes the closely related genus *Atalophlebia.* Tables 46 and 47 show the proportion of each of these animals in the stomach contents of the fish examined in each month of the investigation. Since the changes in feeding habits associated with increasing size and age of the fish are largely complete by the second winter, all fish older than the 1939 year-class have been grouped together in order to increase the size of the samples. The tables show some striking changes in the occurrence of the various animals; the percentage of *Deleatidium* in the food of the fish is initially high, but decreases rapidly during the first year and thereafter fluctuates about a relatively low level; *Olinga* is virtually absent from the food at first, but rapidly increases in importance during the second year and ultimately makes up a very large proportion of the food; the other three Trichoptera larvae are all of little importance during the first year, but rapidly increase during the first half of the second summer, and thereafter appear to show seasonal fluctuations. To assist in the interpretation of these changes the tables also show the approximate percentages of the same animals in the corresponding bottom fauna. These have been derived from the estimated faunas given in Appendix I, but on account of the marked variations in the fauna of the various parts of the stream these mean values have been weighted in proportion to the number of food animals in the fish taken from each zone in the same month. In the months when no faunistic collections were made, approximate values have been obtained by interpolation. These percentages in the fauna obviously do not show changes parallel to those which occurred in the stomach contents, and the fluctuations are largely irregular and often arise from the different degrees of weight which have had to be given to the different zones. The ratio between the two percentages—the availability factor or forage ratio referred to above—has therefore been calculated in each case and is shown in the tables. This shows fluctuations which follow fairly closely those in the composition of the stomach contents, but which are not

TABLE 46. The percentage in the food and in the bottom fauna, and the mean weight, for each of the five main food animals for each month; also the forage ratios and the relative forage ratios compared to *Deleatidium* for each animal in each month; combined results for all zones for fish of the 1939 year-class.

	1939.		1940.												1941.									
	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.
Number of fish ..	57	2	20	22	3	26	9	0	27	12	24	18	25	22	21	23	19	7	8	12	5	0	14	7
Number of food organisms	431	47	327	786	100	813	298	0	1,378	810	2,439	1,242	2,715	3,790	2,023	671	1,059	166	361	638	58	0	1,099	275
Helicopsyche—																								
Percentage in food ..	0	0	0·6	0·1	0	1·4	0	..	0·7	0·1	18·2	12·8	28·6	17·2	18·6	6·4	2·0	3·6	0·3	1·3	0	..	2·3	1·8
Percentage in fauna	22·2	62·0	28·5	44·8	0·8	26·2	8·3	..	31·4	8·3	39·7	44·8	30·8	21·3	36·9	35·1	32·2	48·2	16·3	33·3	3·2	..	32·3	41·8
Forage ratio ..	0	0	0·02	0	0	0·05	0	..	0·02	0·01	0·46	0·29	0·93	0·81	0·50	0·18	0·06	0·07	0·02	0·04	0	..	0·07	0·04
Relative ratio ..	0	0	0	0	0	0·01	0	..	0	0	0·21	0·06	1·79	1·17	0·67	0·34	0·02	0·02	0·07	0·01	0	..	0·17	0·11
Mean weight (mg.) ..	..	0·88	..	..	..	0·56	..	0·59	..	0·84	..	1·12	..	2·37	..	0·83	..	0·45	..	..	..	..	..	0·53
Olinga—																								
Percentage in food ..	0	0	0	0·1	0	0·2	1·0	..	0·8	3·9	3·9	6·1	13·3	4·0	12·4	49·4	28·5	4·6	46·3	16·8	44·9	..	63·7	66·2
Percentage in fauna	1·5	0·9	0·7	1·0	0·5	7·8	1·1	..	2·8	1·4	2·2	2·2	2·5	2·1	2·4	7·8	2·0	0·4	0·9	0·5	1·1	..	1·0	1·2
Forage ratio ..	0	0	0	0·10	0	0·03	0·91	..	0·29	2·78	1·77	2·78	5·33	1·91	5·17	6·34	14·25	11·50	51·5	33·6	40·8	..	63·7	55·2
Relative ratio ..	0	0	0	0·01	0	0·01	0·25	..	0·05	0·92	0·83	0·60	10·25	2·76	6·90	11·95	4·90	3·24	177·5	11·1	16·0	..	154·0	149·0
Mean weight (mg.) ..	..	1·10	..	..	..	1·10	..	1·10	..	1·10	..	1·10	..	1·10	..	1·10	..	1·10	..	..	..	..	..	1·10
Sericostomatid: Type "C"—																								
Percentage in food ..	0	0	0	0	0	0·1	0	..	6·7	3·8	20·7	7·9	7·4	3·1	4·6	3·3	1·8	0	0·3	10·6	0	..	3·5	1·8
Percentage in fauna	1·8	11·2	6·8	11·7	0·2	6·2	4·7	..	5·0	3·0	4·6	4·9	4·8	3·2	10·6	21·9	20·4	21·6	13·8	20·9	1·0	..	17·4	15·1
Forage ratio ..	0	0	0	0	0	0·02	0	..	1·34	1·27	4·49	1·61	1·54	0·97	0·43	0·15	0·09	0	0·02	0·51	0	..	0·20	0·12
Relative ratio ..	0	0	0	0	0	0	0	..	0·26	0·42	2·10	0·35	2·96	1·41	0·57	0·28	0·03	0	0·07	0·17	0	..	0·48	0·32
Mean weight (mg.) ..	..	0·63	..	..	..	0·21	..	0·38	..	0·80	..	0·64	..	0·63	..	0·21	..	0·20	..	..	..	..	..	0·52
Pycnocentrodes—																								
Percentage in food ..	0·2	0	0·6	1·7	3·0	0·4	0	..	0·7	12·2	20·6	22·0	36·4	51·5	25·3	9·5	5·6	0·6	0·6	0·5	1·7	..	1·7	6·2
Percentage in fauna	7·4	4·5	9·0	12·0	3·1	5·0	4·4	..	8·4	5·7	8·7	9·6	14·0	9·4	7·4	3·1	2·6	3·8	7·1	4·6	6·8	..	7·2	8·1
Forage ratio ..	0·03	0	0·07	0·13	0·97	0·08	0	..	0·08	2·14	2·37	2·29	2·60	5·48	3·42	3·07	2·16	0·16	0·09	0·11	0·25	..	0·24	0·76
Relative ratio ..	0·01	0	0·01	0·01	0·16	0·02	0	..	0·01	0·71	1·11	0·50	5·00	7·95	4·56	5·78	0·74	0·05	0·31	0·04	0·10	..	0·58	2·05
Mean weight (mg.) ..	..	0·84	..	..	..	0·24	..	0·25	..	0·36	..	0·58	..	1·33	..	0·51	..	0·23	..	..	..	..	..	0·28
Deleatidium—																								
Percentage in food ..	85·9	91·4	81·1	66·4	92·0	86·1	64·1	..	77·0	35·9	26·1	37·0	6·3	11·6	11·9	6·7	47·2	27·7	5·8	62·1	41·4	..	8·7	6·9
Percentage in fauna	17·0	10·3	7·2	8·1	15·5	20·5	17·6	..	14·0	11·9	12·2	8·0	12·2	16·7	15·9	12·6	16·2	7·8	20·3	20·6	16·2	..	21·0	18·4
Forage ratio ..	5·06	8·87	11·28	8·17	5·94	4·21	3·64	..	5·50	3·02	2·14	4·62	0·52	0·69	0·75	0·53	2·91	3·55	0·29	3·01	2·56	..	0·41	0·37
Mean weight (mg.) ..	..	0·49	..	..	..	0·44	..	0·32	..	0·53	..	0·32	..	0·39	..	0·24	..	0·22	..	..	..	..	..	0·34

related to the variations in the fauna. It is evident therefore that the variations in the composition of the food are mainly due to changes in the relative extent to which the various components are eaten. The ratio shows, though less clearly, the same three types of variation which were seen in the percentage composition of the stomach contents; *Deleatidium* falls during the first year from an initially high value, and thereafter fluctuates about a lower level; *Olinga* has a very low value during the first year and thereafter rises rapidly to an extraordinarily high level; the other three Trichoptera larvae have low values during the first year and thereafter show marked seasonal fluctuations with values which are high in early summer and low in early winter. It has previously been shown (Allen, 1942) that there is a general tendency among salmonid fish for the forage ratios of soft-bodied animals, such as Ephemeroptera nymphs and Chironomid larvae, to be high for small fish and to decrease as the fish grow, while the reverse occurs for hard-shelled or cased animals, such as molluscs and Trichoptera larvae. It is evident that the fluctuations described above fall within this general pattern, although some other explanation must be sought for the seasonal variations shown by three of the Trichoptera larvae. Since it was noticed that the larvae found in the trout stomachs were generally of relatively large size, it seemed worth while to investigate the relation between the ratio and the size of the larvae in each month.

Approximate data for this purpose were available in the form of the mean weights of the larvae taken in the regular faunistic collections which are set out in Appendix II. A combined mean weight for all zones has been determined for each month in which collections were made, as for the other data in Tables 46 and 47. Since the shape of the growth curve is fairly similar in all zones, while the variations in size from zone to zone are relatively large, a simple mean is more suitable than a weighted one in this case. Comparison shows that in the four Trichoptera larvae the variations in size and forage ratio tend to follow parallel courses; *Olinga*, which has a consistently high ratio once the fish begin to eat it freely, has a uniform and relatively large average size throughout the year; in the other three Trichoptera larvae the forage ratio and the average size are both at a maximum in early summer, and are low during the winter. In Fig. 12 the mean size and forage ratios are plotted against time for *Deleatidium* and the three Trichoptera larvae which show seasonal changes. It is evident that the correspondence between the two curves is extremely close for all the Trichoptera and that the forage ratio rises rapidly at the same time that the average weight of the larvae is approaching its maximum. In *Helicopsyche* and *Pycnocentrodes* larvae the maximum is of short duration and occurs about December in both curves. In Sericostomatid type "C" the maximum size is reached much earlier, about August, and a high level is maintained for a much longer period than in the other two forms; the forage ratio rises to its maximum correspondingly early, but it also declines fairly rapidly, and has reached low values again by December, when the mean size is still high. In contrast to the three forms just discussed *Deleatidium* seems to show small random fluctuations in average size; the forage ratio on the other hand after the initial decrease shows signs of seasonal fluctuations which are in opposition to those shown by the Trichoptera. An explanation of this effect as well as of the quick decrease in the ratio for Sericostomatid type "C" larvae can be found if the nature of the ratio is examined further. The consistency of the results which have been obtained with

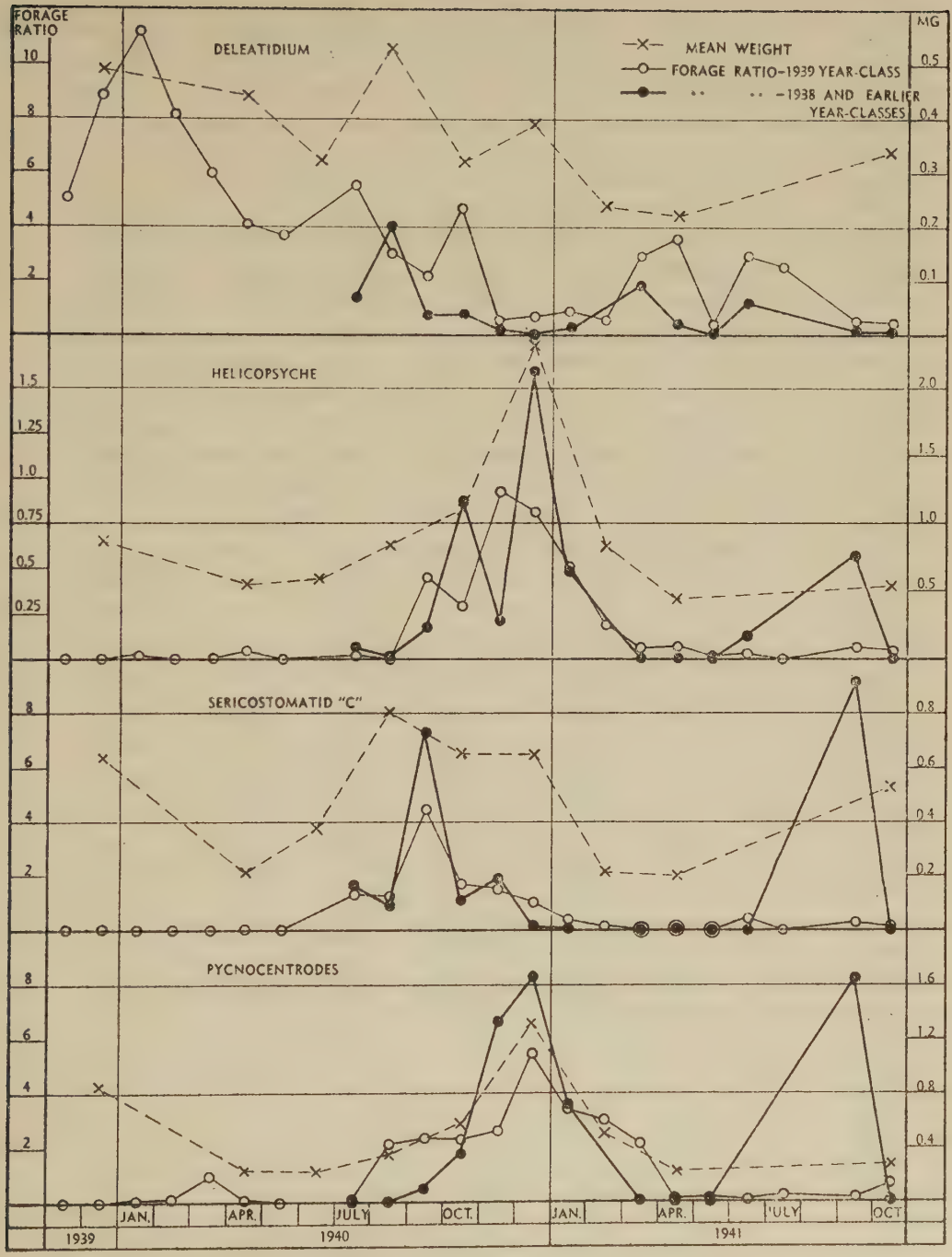

FIGURE 12. Comparison, for *Deleatidium* and three species of Trichoptera larvae, between the mean weight and the forage ratios determined for fish of the 1939, and the 1938 and earlier year-classes.

TABLE 47. The percentage in the food and in the bottom fauna for each of the five main food animals for each month; also the forage ratio and the relative forage ratios compared to *Deleatidium* for each animal in each month; combined results for all zones of the fish of the 1938 and earlier year-classes.

	1940.						1941.									
	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.
Number of fish	19	3	10	9	11	12	7	0	3	2	1	1	0	0	1	1
Number of food organisms ..	1,334	308	1,516	1,477	1,200	2,331	223	0	111	128	36	95	0	0	502	20
Helicopsyche—																
Percentage in food	1·9	0	7·4	44·5	7·5	29·1	9·8	..	0	0·8	0	1·1	..	..	39·8	0
Percentage in fauna	30·6	11·8	42·6	52·0	36·4	18·3	20·0	..	46·9	45·0	9·2	9·2	..	..	68·0	68·0
Forage ratio	0·06	0	0·17	0·86	0·21	1·60	0·49	..	0	0·02	0	0·12	..	..	0·58	0
Relative ratio	0·04	0	0·23	1·12	1·31	17·75	1·15	..	0	0·05	..	0·10	..	..	4·46	..
Olinga—																
Percentage in food	53·5	55·2	23·2	11·6	37·1	8·3	19·7	..	48·7	75·0	63·9	47·3	..	..	8·0	75·0
Percentage in fauna	2·0	1·5	3·1	2·5	2·0	1·5	4·2	..	3·2	0·1	0·9	0·9	..	..	1·3	1·3
Forage ratio	26·75	36·8	7·48	4·64	18·55	5·53	4·68	..	15·20	750·0	71·0	52·6	..	..	6·53	57·7
Relative ratio	16·9	9·28	10·1	6·02	116·0	61·5	12·00	..	83·5	1,700·0	++	46·3	..	..	50·4	++
Sericostomatid : Type "C"—																
Percentage in food	13·3	4·2	42·7	4·4	7·5	0·4	0·4	..	0·9	1·6	0	0	..	..	41·0	0
Percentage in fauna	7·4	4·5	5·8	4·0	4·0	2·3	9·9	..	19·0	17·7	16·8	16·8	..	..	4·5	4·5
Forage ratio	1·79	0·93	7·35	1·10	1·87	0·17	0·04	..	0·05	0·09	0	0	..	..	9·14	0
Relative ratio	1·13	0·23	9·92	1·43	11·7	1·89	0·10	..	0·03	0·20	..	0	..	..	70·3	..
Pycnocentrodes																
Percentage in food	0·5	0	7·2	21·0	39·8	55·0	14·8	..	0	0	0	0	..	..	6·6	0
Percentage in fauna	9·1	4·9	13·5	11·4	6·0	6·6	4·1	..	4·6	4·3	7·9	7·9	..	..	0·8	0·8
Forage ratio	0·06	0	0·53	1·84	6·63	8·33	3·61	..	0	0	0	0	..	..	8·25	0
Relative ratio	0·04	0	0·72	2·39	41·4	92·5	9·25	..	0	0	..	0	..	..	63·5	..
Deleatidium—																
Percentage in food	22·7	35·7	8·1	8·9	2·4	1·6	6·3	..	19·8	10·9	0	25·3	..	..	2·8	0
Percentage in fauna	14·5	9·0	10·9	11·5	15·2	17·1	16·1	..	10·9	24·8	20·7	20·7	..	..	20·9	20·9
Forage ratio	1·57	3·97	0·74	0·77	0·16	0·09	0·39	..	1·82	0·44	0	1·22	..	..	0·13	0

this ratio in this and other work demonstrates clearly that it is in some way a measure of the extent to which the particular organism is eaten by the fish concerned. Whatever the mechanism governing the taking of its food by the fish, it will be the habits and physical properties of the food-organism, its size, appearance, taste, etc., which will determine how freely it is eaten. The ratio is therefore a measure of these properties, and for all series of food-organisms the ratios for any particular forms should stand in the same relation to each other, whatever the proportions in which they occur in the fauna. It has been shown in earlier discussions of this subject (Allen, 1941) that the actual ratios on the other hand will vary with the composition of the fauna. It can be shown that if A_1, A_2, A_3, etc. are the values of the ratio on any standard scale for animals forming P_1, P_2, P_3, etc. in the fauna, then the forage ratio for every animal in the fauna is related to the corresponding ratio in the standard scale by the ratio $1 : \Sigma AP$. It follows from this that as the proportion in the fauna of animals with relatively high ratios increases the forage ratios of the individual forms as determined from that particular fauna will decrease. When the trout have reached sufficient size to be able to eat cased caddis larvae freely, and when the larvae themselves are large enough to be attractive to the trout, the relative values of A for these larvae are increased; ΣAP therefore increases and the actual forage ratios of the forms whose availability and attractiveness to the trout have not altered are decreased. It is probably this effect which causes the forage ratio of *Deleatidium* to decrease during the summer despite the absence of any significant change in the size or habits of the nymphs. Similarly when in November and December the larvae of *Helicopsyche* and *Pycnocentrodes* reach the size at which they are freely eaten, the value of ΣAP increases again and the forage ratios of such forms as Sericostomatid type "C" which have remained at the same level of availability and attractiveness are reduced.

Further analysis of these relationships would require the development of means whereby the extent to which a particular form was eaten could be studied without the complication of the fluctuations caused by the changes in the composition and characteristics of the remainder of the fauna. There appear to be two means of approach to this problem; in an earlier paper (Allen, 1941a) an attempt was made to define the "absolute availability" of every potential food-organism; this was defined as "the proportion of the population which in a typical habitat would be visible to and of suitable size and taste to be eaten by a fish of the species under consideration if the fish had the whole area under observation." If means could be developed of assessing directly the combined effect of the various factors upon which this absolute availability would depend, this would provide a very valuable reference scale with which forage ratios could be compared. At present, however, a more practical method seems to be to compare the forage ratios with some comparable quantity whose absolute value is likely to remain constant from one comparison series to another. Such a basis for comparison would be provided by the forage ratios in successive series of a food animal which appears unlikely to have changed significantly in its availability or attractiveness from one series to the next. Such a reference animal must have at least the following properties; it must be reasonably abundant and be eaten sufficiently freely to occur in large enough numbers in both faunistic collections and stomach contents to keep sampling

errors to a minimum; it must remain at about the same level of abundance throughout the period of observation so as to avoid effects due to any non-linearity in the relation between the proportions in food and fauna; it must not undergo any significant changes in average size during the period and should preferably be present at all times in a good range of sizes; it should not undergo any significant changes in habit during the period; it should not be gregarious as this would greatly increase sampling errors. There is, in the Horokiwi fauna, only one group which complies even approximately with these requirements. This is *Deleatidium* which does however appear to fill the requirements sufficiently well to make it worth while to examine the possibilities of the technique. Tables 46 and 47 therefore show for each month the relative forage ratio of each of the four Trichoptera larvae when compared with *Deleatidium*. The seasonal changes are very similar to those for the original forage ratios although the range of variation for each form is considerably extended. It is interesting to note, however, that the relative forage ratio for Sericostomatid type "C" develops a double peak which corresponds more closely to the flat top of the size curve than did the sharp single peak of the original forage ratio curve. When it is considered that this method has introduced a second set of sampling errors by adding those for *Deleatidium* to those obtained for each of the Trichoptera, it is surprising that more irregularities do not appear.

Tables 46 and 47 show that the five main food animals made up at least half, and generally between 85 per cent. and 95 per cent., of the total stomach contents in every month. The other animals, even though abundant in the fauna, occurred in the stomach contents in relatively small numbers, and consequently the sampling errors involved in the determination of their forage ratios are comparatively high.

In the preceding paragraphs the results of all zones have been grouped together without regard for differences in the composition of the fauna, but it is also desirable to examine the effect of such differences on the forage ratios. In order to reduce sampling errors as much as possible, while subdividing the data according to zones, it is necessary to group the results of several months together. Since very pronounced variations with time occur, grouping has to be restricted to the extent which is possible without allowing the seasonal changes to interfere with the effects due to other causes. It appears in consequence that the data can be most satisfactorily grouped into six-month periods, centred on mid-summer and mid-winter respectively. The first of these corresponds as closely as is practicable with the period within which the Trichoptera larvae have their maximum ratio, while the winter period corresponds to the Trichoptera minimum. Table 48 therefore shows the mean forage ratio for all components of the fauna listed in Appendix I in each zone in each six-month period. The only forms omitted are the pupae of *Pycnocentrodes* and Sericostomatid type "C" and of Simuliidae, none of which was ever recorded in the stomach contents. Examination of the table shows that none of the forms which vary in abundance in different parts of the stream, such as *Helicopsyche* and Sericostomatid type "C," which are most numerous in the upstream zones, or Parnidae and *Potamopyrgus*, which are most abundant downstream, shows any correlated pattern in the local distribution of their availability factors. The table therefore includes mean forage ratios for each

form; these are the simple averages of the values found for that six-month period in the five zones. All determinations based on percentages in the bottom fauna of less than 1 per cent. are marked with an asterisk (*) since in these cases the small number found in the samples may lead to large sampling errors. They have however been included in the averages unless they are very different from other comparable values. The few divergent values which have been omitted from the averages are italicized in the table.

TABLE 48. The forage ratios of each of the main constituents of the bottom fauna in each zone in each six-months period. The asterisk (*) indicates that the value is based on a bottom fauna percentage of less than 1 per cent.; the figures in italics have been omitted from the period means.

FOOD ANIMAL.	Zone	1939 YEAR-CLASS					PRE-1939 YEAR-CLASSES.		
		Oct. 39–Mar. 40.	Apr. 40–Sept. 40.	Oct. 40–Mar. 41.	Apr. 41–Sept. 41.	Oct. 41.	Apr. 40–Sept. 40.	Oct. 40–Mar. 41.	Apr. 41–Sept. 41.
Hydropsyche	I	1·39	0·61	0·20	0·33	..	0·15	1·47	..
	II	..	0·20	0·12	0·06*	1·43*	0·44*	0·57	0
	III	0	1·80*	0·11*	0*	..	0·50*	0·50*	..
	IV	0·08	0·12*	0·06	0·40	1·08	1·33*	0·15	0·04
	V	0·25	1·00	0·10	0·95	..	0·50*	0	0·84
	Mean	0·43	0·75	0·12	0·35	1·25	0·58	0·54	0·29
Rhyacophilidæ larvæ	I	1·75*	4·80*	0·12*	3·00*	..	2·50*	0·14*	..
	II	..	0·44*	1·27	3·00*	1·11*	1·22*	0	0*
	III	11·37*	2·29*	0·87*	*22·00**	..	1·00*	0·17*	..
	IV	2·00*	3·75*	0·27*	2·00*	1·44*	3·25*	0·17*	0*
	V	1·37*	3·33*	0·56*	6·00*	..	0·50*	0*	0*
	Mean	4·12	2·92	0·62	3·50	1·27	1·69	0·10	0
Rhyacophilidæ pupæ	I	..	0*	0·75*	0*	..	0*	0*	..
	II	..	0*	0·12*	0*	0*	0·33*	0·56*	0*
	III	..	0*	0*	0*	..	0*	0*	..
	IV	..	0*	0*	0*	..	0*	0*	0*
	V	..	0*	0*	..	..	0*	0*	..
	Mean	..	0	0·17	0	0	0·07	0·11	0
Helicopsyche	I	0·25*	0·35	0·08	0·37	..	0	0·36	..
	II	..	0·28	0·73	0·02	0	0·04	1·74	0·08
	III	0	0·15	0·62	0	..	0·12	0·73	..
	IV	0	0·41	0·40	0·10	0·04	0·19	0·73	0·85
	V	0·01	0·04	0·74	0·06	..	0·18	0·48	0·02
	Mean	0·06	0·25	0·51	0·11	0·02	0·11	0·81	0·19
Olinga larvæ	I	0*	0·70	1·47*	161·00*	..	46·60	0·57*	..
	II	..	3·47	4·40	57·00	127·57*	34·80	7·85	57·70*
	III	0*	0·13	2·10	48·90	..	5·64	6·04	..
	IV	0·33*	0·92	14·34	82·67*	59·45	14·20	10·60	17·83
	V	0	0·15	3·47	203·00*	..	9·06	12·14	750·0*
	Mean	0·08	1·07	3·16	110·51	93·51	22·06	7·44	165·0
Sericostomatidæ: Type "C" larvæ	I	0*	2·00*	*10·5**	*31·00**	..	1·00*	1·00*	..
	II	..	2·52	0·96	0·14	0·04	2·59	1·19	0
	III	0	1·66	0·93	0·07	..	5·85	0·58	..
	IV	0	2·56	0·12	0·14	0·89	0·93	0·67	1·38
	V	0	0·04	0·35	0·72	..	1·51	0·08	0·09
	Mean	0	1·76	0·59	0·27	0·46	2·38	0·70	0·49
Pycnocentrodes larvæ	I	0·32	2·21	8·13	0·21	..	0·45	13·48	..
	II	..	1·71	6·96	0·08	0	0·44	5·56	0
	III	0	1·16	1·13	0·32	..	0·30	1·17	..
	IV	0·13	2·90	7·64	1·07	0·34*	1·05	5·85	4·20
	V	0·02	0·06	1·84	0·37	..	0·26	0·48	0
	Mean	0·12	1·41	5·14	0·41	0·17	0·52	5·31	1·40
Coloburiscus	I	0*	1·00*	0·17*	0·25	..	10·00*	0·25*	..
	II	..	1·40	0·33*	0	0	0*	0·50*	0
	III	0*	3·33*	2·67*	0*	..	9·33*	9·00*	..
	IV	1·25*	3·00*	1·33*	3·00*	0	15·50*	0·25*	1·00*
	V	0	1·07	0·60*	9·00*	..	22·20*	3·50*	0*
	Mean	0·31	1·96	1·02	2·45	0	11·41	2·70	0·33
Deleatidium	I	16·45	3·86	0·17	0·41	..	1·65	1·73	..
	II	..	3·11	0·40	0·89	0·22	1·83	0·27	0·88
	III	22·15	4·91	1·67	2·52	..	0·45	0·77	..
	IV	8·02	2·46	2·83	1·85	0	2·03	0·22	0·17
	V	8·25	4·26	1·18	1·69	..	0·88	0·75	4·40
	Mean	13·72	3·68	1·25	1·47	0·11	1·37	0·75	1·82
Leptoperlidæ	I	..	1·00*	0*	0*	..	0*	0*	..
	II	..	2·00*	0*	0*	..	0*	..	0*
	III	0*	2·50	0·16	0·35	..	0·14	0·70	..
	IV	2·00*	1·00*	0	..	..	1·50*	0*	+
	V	2·00*	1·33*	0*	..	..	0*	0*	..
	Mean	1·00	1·37	0·03	0·11	..	0·33	0·18	+

Food Animal.	Zone.	1939 Year-class. Oct. 39–Mar. 40.	Apr. 40–Sept. 40.	Oct. 40–Mar. 41.	Apr. 41–Sept. 41.	Oct. 41.	Pre-1939 Year-classes. Apr. 40–Sept. 40.	Oct. 40–Mar. 41.	Apr. 41–Sept. 41.
Parnidæ imagines	I	0*	0*	16·50*	0*	..	0*	0·60	..
	II	..	..	3·50*	0*	..	..	6·00*	0*
	III	0*	0*	3·50*	..	..	..	..	..
	IV	0*	..	+	..	..	..	8·00*	..
	V	0*	..	4·50*	0*	..	..	0*	0*
	Mean	0	0	7·00+	0	..	0	3·65	0
Parnidæ larvæ	I	0	0*	0	0	..	0	0	..
	II	..	0	0·01	0	0	0	0·02	0
	III	0	0	0	0	..	0	0	..
	IV	0	0*	0	0	..	0*	0	0
	V	0·01	0	0	0	..	0	0	0
	Mean	0	0	0	0	0	0	0	0
Chironomidæ larvæ	I	11·50*	0·02	0	0	..	0·01	0	..
	II	..	0·36	0·01	0	0	0	0	0
	III	0	0	0·10	0*	..	0	0·25	..
	IV	35·0*	0·07	0·33	0*	..	0	0·04	..
	V	73·0*	0	0·10	0·11	..	0	0	0
	Mean	29·9	0·09	0·11	0·02	0	0	0·06	0
Chironomidæ pupæ	I	+	0·19	0	0*	..	0	0	..
	II	..	0·27	0·06	0·12	0	0	0·02	0
	III	..	0*	0*	..	..	0*	0*	..
	IV	+	0·11*	0*	..	..	0*	0*	..
	V	+	0·50*	0*	..	..	0*	0*	..
	Mean	+	0·21	0·01	0·06	0	0	0	0
Simuliidæ larvæ	I	+	1·00*	0*	0*	..	0*	0*	..
	II	..	0	0*	0*	..	0	0*	0*
	III	..	..	..	..	..	..	..	..
	IV	..	..	..	..	..	..	..	..
	V	+	0*	+	..	..	0*	0*	..
	Mean	+	0·33	+	0	..	0	0	0
Other Diptera larvæ	I	2·00*	0·20*	0	0*	..	0*	0	..
	II	..	0*	0·11*	0*	..	0*	0·12*	0*
	III	0*	0*	0·17*	0*	..	0*	0·20*	..
	IV	0*	0·33*	0*	0*	..	0*	0*	0*
	V	0*	0*	0	2·00*	..	0*	0	0*
	Mean	0·50	0·11	0·06	0·40	..	0	0·06	0
Potamopyrgus	I	0	0·09*	1·83	0·66	..	0	0·25	..
	II	..	0·20	4·08	16·68*	0*	0·06	3·00	23·90*
	III	0	0·36	8·09	35·00*	..	0·44	2·58	..
	IV	0	2·06	17·33*	9·00*	0*	0·92	6·40	1·00*
	V	0	0·24	6·38	2·67*	..	0·16	0·44	2·67*
	Mean	0	0·59	7·54	12·80	0	0·32	2·53	9·19
Latia ..	I	..	..	..	0*	..	0*	..	..
	II	..	..	..	..	..	..	..	..
	III	0*	0·07	1·00*	0*	..	0·15	0·60*	..
	IV	0*	0*	2·00*	12·00*	..	0*	2·00*	0*
	V	0*	0*	..	..	..	0*	4·00*	..
	Mean	0	0·02	1·00	4·00	..	0·04	2·20	0
Oligochaeta	I	0*	0	0·09	0	..	0	0	..
	II	..	0*	0*	0*	..	0*	0*	0*
	III	..	0*	..	0*	..	0*	*7·00**	..
	IV	0*	0*	0*	..	0*	0*	0*	0*
	V	0*	0*	0*	0*	..	0*	0*	0*
	Mean	0	0	0·02	0	0	0	0	0
Number of fish	I	44	22	16	9	0	6	5	0
	II	0	35	46	15	3	10	15	2
	III	1	10	18	3	0	6	7	0
	IV	44	19	31	12	1	6	12	2
	V	16	11	17	7	0	4	4	2
	Total	105	97	128	46	4	32	43	6

In earlier work on the food of young salmon it was suggested that the animals of the bottom fauna could be divided into four categories according to their forage ratios, and that these categories also divided the animals according to their habits and appearance. The categories used were: high ratios of 2.0 or more: medium, 0.5 to 1.5: low, less than 0.5: and zero. These categories can be effectively applied to the present results with the addition of certain subdivisions which arise from the much greater size range of the fish studied and from the additional

seasonal effects which occur in this instance. The following categories seem to be appropriate:

1. Ratio high (greater than 2.0) at some period during the life of the fish.

   (a) Very high for young fish, but falling rapidly to very low values thereafter; includes Chironomidae and Simuliidae.

   (b) High for young fish but falling to moderate values thereafter; includes *Deleatidium* and probably Rhyacophilidae larvae.

   (c) Low or zero at first but rising to high levels for fish in their second and later years; these may be subdivided into:—

      (1) Value, once risen, remains high, e.g. *Olinga, Potamopyrgus* and perhaps *Latia*.

      (2) Seasonal fluctuations occur; these may be due to size changes in the food-organism, as in *Helicopsyche, Pycnocentrodes* and Sericostomatid type "C," or to the virtual absence of the food-organisms from both fauna and food at certain seasons, as in Parnidae imagines.

2. Ratio moderate (0.5 to 1.5).
   The main forms occurring in this group are *Hydropsyche* larvae and Leptoperlidae nymphs. The former would appear to have more or less constant values throughout life, while the latter shows a decrease in the older fish. *Coloburiscus* may also belong in this group.

3. Ratio low (0 to 0.5) at all times.
   This includes Rhyacophilidae pupae, Parnidae larvae, other Diptera larvae and Oligochaeta.

When the characteristics of the animals falling into these categories are considered, they appear to have certain features in common apart from their taxonomic position. The animals in Group 1 which are eaten freely at some time in the life of the fish are all forms which normally live on the exposed surfaces of stones and plants, and most of them are active in their habits or conspicuous in their appearance, or both. Those in Groups 1a and 1b, which are eaten most freely by small fish, are soft-bodied, unprotected forms, and those eaten by the smallest fish are particularly small animals. On the other hand, the animals which are more freely eaten by the larger fish are all protected either by shells or by built-up cases. The animals in Group 2 which are less freely eaten tend to be rather less active in their habits and to live more in crevices and under stones. The Group 3 animals, which are rarely if ever eaten, include mainly burrowing forms which would normally be inaccessible to a fish like the trout, which in stony streams usually feeds on the surface of the stream bed rather than by grubbing into it. The general results therefore support the principles which have been set out in previous papers; that the extent to which any particular food-organism is eaten depends primarily on the extent to which its appearance and habits make it visible to the trout, and that the larger the trout the more freely does it eat the larger animals, and those protected by hard shells or cases.

Although it appears that the extent to which each type of animal in the bottom fauna is eaten depends upon its availability to the fish, the data as presented above provide no indication as to whether the fish are actually feeding at random on the animals which are visible, and available to them, or whether the fish are by some means exercising selection from among these animals. It is for this reason that it has been considered preferable in the present case to use the purely descriptive term "forage ratio" for the ratio between proportion in food and proportion in fauna, rather than the term "availability factor" which has implications as to the mechanism leading to the differences in the ratio for different food animals.

In a previous study of the feeding habits of young salmon (Allen, 1941a) it was shown that the proportional composition of the stomach contents tended to change as the number of animals in it increased. At first the average percentage made up by the most numerous animal decreased, and it was shown that the curve closely followed that which would occur if the fish were feeding at random. Beyond a total of about five animals in the stomachs, however, the proportion of the most numerous animal increased again, and finally appeared to level off at values between 80 per cent. and 90 per cent. This effect was ascribed to selection by the fish of a particular food-organism when they had been feeding for some time. A rather similar effect has recently been found by Burnet (in press) to occur in the New Zealand eel, *Anguilla dieffenbachii*. In the work on salmon advantage was taken of this effect to eliminate those fish which had apparently been exercising selection, and the ratio then determined from the stomach contents of fish containing only a few animals was considered to be principally a measure of the availability of the various animals to the fish and could therefore be appropriately termed the "availability factor."

TABLE 49. The variation in the percentage of the dominant or most numerous animal with the total number of animals in the trout stomachs. Results shown separately for two parts of the life of the 1939 year-class, and for older fish.

Year-class	Period.		Total Number of Animals in Stomach. 1.	2–5.	6–10.	11–20.	21–30.	31–40.	41–50.	51–70.	71–100.	101–200.	201.
1939	Oct. 39–June 40	Number of fish ..	2	29	27	34	16	10	12	0	1	2	0
		Percentage dominant ..	100	89	82	80	84	86	80	..	62	55	..
	July 40–Oct. 41	Number of fish ..	2	12		26	26	24	24	26	41	40	16
		Percentage dominant ..	100	64		62	58	50	54	61	64	61	59
1938 and earlier	Total	Number of fish ..	0	4		6	6	5	6	18	11	9	15
		Percentage dominant ..	..	51		67	64	47	54	57	61	63	70

Since it is clearly desirable to distinguish if possible between the effects due to random feeding and those due to selection, the data obtained from the Horokiwi trout have been examined by the methods described above. The results are shown in Table 49. Close examination of the data showed that a somewhat abrupt change took place during the first winter and that the average percentage made up by the most numerous food-organism in the stomachs was very much higher before this time than it was at any time afterwards. This change occurred almost simultaneously with the appearance of the Trichoptera larvae among the food of the trout. It is probably due to the fact that after the addition of the Trichoptera the food

available to the trout consists of a number of more or less equally abundant forms, while before that time it tends to be dominated by only one or two groups. On account of this change the data derived from the 1939 year-class have been divided at the end of June, 1940, into two parts. The data for the 1938 and earlier year-classes, being derived entirely from older fish, have been treated as a whole. The table shows that in the young trout the proportion of the most numerous animal drops rapidly at first, and thereafter is relatively stable at about 80 per cent. and that changes similar to those found in the salmon do not occur. The few fish with more than 50 animals in their stomachs had a much lower percentage of the dominant form, but there were so few of them that this may have been a chance effect. The older fish show rather different results; after an initial rapid decline the percentage continues to decrease more slowly until it is a little under 50 per cent. in fish with 31–40 animals in their stomachs; thereafter it rises again and finally becomes steady at about 62 per cent. It is evident however that the great majority of fish in both age-groups have stomach contents which are very similar in composition. Whether selection has played a part in the process, or whether it has been due solely to random feeding, there appears to be no possibility of dividing the material into two parts and so attempting to isolate the availability and selection effects by the methods which could be applied to the young salmon. The forage ratio is therefore simply a means of describing the final result of all the factors which determine the extent to which any particular food animal is eaten by the trout.

Tables 47 and 48 show clearly that there is one form which gave much higher forage ratios than any of the others. This was *Olinga*, which regularly gave values of 50 or more for the older trout. Two other forms which occurred so rarely in the faunistic collections as to be omitted from the tables were also sometimes found in considerable numbers in the trout stomachs; these were the small amphipod *Paracalliope*, which was freely eaten by trout in their first few months, and a Trichoptera larva, apparently closely related to *Olinga*, which was frequently found in the stomachs of older trout.

General observations suggest that all these three forms, which were relatively scarce in the shingle of the stream bed where the faunistic collections were made, were much more common in cress and fringing grasses along the margins of the stream which were not examined in the quantitative faunistic work, and that the trout were obtaining them from this source. In the studies made on the food of young salmon in England and Scotland (Allen, 1941a), it was also found that one group of animals yielded peculiarly high availability factors; these were the Hydroptilidae larvae, which were very scarce in the faunistic collections, but frequently yielded availability factors greater than 100. It seemed likely in that case also that the faunistic sampling methods which were used did not give an adequate indication of the abundance of this particular form.

The forage ratios in this work have been based on faunas which have the estimated mean composition for the whole of the zone concerned, including an allowance for the proportion of each type of water in the zone. A feeding trout however had before it not a fauna of the composition shown in the table, but one appropriate to the particular type of water in which it was feeding, and it has been

shown that some of the animals of the bottom fauna differ considerably in their abundance in waters of different types. The forage ratio, as determined above, does however provide a measure of the extent to which the whole population of a food animal in a zone is preyed upon by trout.

In previous sections of this paper much attention has been given to the study of the probable errors of the various estimates which have been made. In the present section such an attempt would be exceedingly complex, because not only are sampling errors being introduced in both the faunistic studies and in stomach contents, but also the data are, particularly in the latter case, very irregular, due to variations in the numbers of fish available for examination, and especially to the very variable numbers of animals present in the stomachs of the fish. An indication of the reliability of the results can however be gained from Table 48. This indicates that the fluctuations due to sampling errors or unidentified effects which occur from zone to zone within periods in which there is no major change are generally small compared with the differences which occur between different food animals, or which arise from growth of either fish or food animals. The consistency of the results seems therefore quite sufficient to allow considerable confidence to be placed in these inter-specific and growth differences. The rather erratic results obtained at the end of the period of observations, and particularly in September and October, 1941, are probably mainly due to increased sampling errors arising from the small number of fish which could be obtained for examination.

(c) Gravimetric Results

While the numerical method provides a useful technique for examining the extent to which the various animals of the bottom fauna are eaten by trout, it is less satisfactory for studying the relation between the amount of food taken and the rate of growth and the productivity of the trout population. For this purpose the determination of the weight of food found in each stomach is preferable, since it is less subject to variations due to differences in the size of the individual food-organisms. To obtain these data, the contents of each stomach were dried and weighed by the methods described above. Where a particular organism appeared of special significance it was weighed separately, but normally only the total weight of the stomach contents was recorded.

Although the stomach contents of the Horokiwi trout consisted mainly of the invertebrates of the bottom fauna they also included surface food and small fish. Surface food made up less than 5 per cent. of the total number of organisms in the stomachs, and since the animals composing the surface food are generally similar in size to those taken from the bottom fauna the actual mass of food obtained from the surface is probably also less than 5 per cent. of the total food intake. The number of small fish taken forms an even smaller proportion, being about 0.06 per cent. of the organisms in the stomachs of trout old enough to be feeding on small fish. This figure however gives a misleading impression of the significance of this kind of food. About 5 per cent. of the trout examined in or after September of their second year contained small fish, and the estimated live weight of the food fish averaged about 0.74 per cent. of the weight of the trout. It will be shown later that in trout two years or more in age the estimated live

weight of the stomach contents is generally between 0.1 and 0.2 per cent. of the weight of the trout. Those which had eaten smaller fish had therefore, on the average, about five times as much food in their stomachs as those which had been feeding on the bottom fauna or at the surface. Although the samples are too small to have any great significance, the most probable estimate of the proportion of small fish by weight in the total stomach contents of Horokiwi trout of two years or more is therefore:

$$\frac{5 \times 5}{95 + 5 \times 5}$$

or approximately 20 per cent. This can also be considered as an estimate of the proportion of small fish in the food consumed by the older trout, but since it seems very probable that the time for passage through the stomach will be greater for the relatively large fish than for the invertebrates, 20 per cent. is likely to be a maximal estimate of the proportion of small fish in the food consumed. The final conclusions are therefore that the food of Horokiwi trout consists in the first two years of at least 95 per cent. of bottom fauna and less than 5 per cent. surface food; in later years it consists of at least 75 per cent. bottom fauna, less than 20 per cent. small fish and less than 5 per cent. surface food. In view of the magnitude of the errors which have been shown to occur in the estimates of the trout and bottom fauna populations, it is evident that at least the surface food can be ignored in considering the relation between the amount of food taken by the trout and the supplies available.

Consideration must also be given to variations in the amount of food in the stomachs of the trout in different parts of the stream and at different ages. The results of analysis for these effects are summarized in Tables 50 and 51, and the combined results for all zones are plotted in Fig. 13.

It is evident from the tables that there are no regular differences of significant size between the amounts of food taken by the fish in the different zones, although there are random variations due to the small size of the samples, and the large individual differences among the fish. There are, on the other hand, very definite variations with time. The dry weight drops rapidly from an initial value of over 50 p.p. 10^4 to about 15 by the middle of the first winter; it rises again to a peak of about 25 early in the following summer, and then declines again. The results for the older fish show that the alternation between summer maxima and winter minima continues throughout life.

It has been shown that the nature of the food of the Horokiwi trout changes during the life of the fish. It consists at first entirely of unprotected, soft-bodied forms, but towards the end of the first year the trout begin to feed increasingly on animals with protective shells and cases, particularly Trichoptera larvae; these dominate the food during the first half of the second summer, but are afterwards gradually replaced by soft-bodied forms; in later years there is a regular alternation between the predominance of Trichoptera larvae in summer and of the Ephemeroptera and other soft-bodied forms in winter. It is obvious that, after the initial decline, the peaks in the dry weight of stomach contents coincide with

TABLE 50. The mean dry weight and estimated wet weight of the stomach contents of the fish of the 1939 year-class taken in each month; results expressed in parts per 10,000 of the live weight of the fish.

Zone.		1939.				1940.												1941.									
		Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.
I	Number of fish	1	0	31	0	6	3	3	6	3	0	5	4	4	0	4	4	5	0	4	0	2	0	3	0	4	0
	Wet weight	224	..	126	..	92	32	76	60	37	..	61	30	33	..	13	41	11	..	10	..	7	..	14	..	15	..
II	Number of fish	0	0	0	0	0	0	0	5	6	0	8	8	8	4	12	7	4	13	6	0	4	4	2	0	4	3
	Wet weight	..	..	..	..	..	..	..	69	54	..	29	38	20	24	17	32	7	9	8	..	12	14	21	..	42	18
III	Number of fish	0	0	1	0	0	0	0	2	0	0	4	0	4	1	4	4	2	2	1	1	2	0	0	0	0	0
	Wet weight	..	..	..	258	..	..	..	71	..	..	48	..	53	37	24	19	16	17	14	38	10	..	..	..	..	..
IV	Number of fish	0	0	19	2	8	15	0	6	0	0	5	0	8	5	3	4	6	5	8	4	0	5	0	0	3	1
	Wet weight	..	..	..	155	96	92	62	..	41	..	..	63	..	25	33	15	20	15	29	28	8	..	17	..	..	32	43
V	Number of fish	0	0	6	0	6	4	0	6	0	0	5	0	0	4	3	3	4	3	0	2	0	3	0	0	2	3
	Wet weight	..	..	..	202	..	53	134	..	50	..	..	54	..	..	32	17	25	17	14	..	7	..	15	..	..	20	12
Total	Number of fish	1	0	57	2	20	22	3	25	9	0	27	12	24	14	26	22	21	23	19	7	8	12	5	0	13	7
	Wet weight	224	..	146	96	80	71	76	56	48	..	49	35	29	30	17	28	13	15	17	12	10	16	17	..	28	18
	Dry weight	56	..	34	22	20	18	21	14	11	..	17	19	28	23	24	41	16	9	8	7	9	7	3	..	29	17

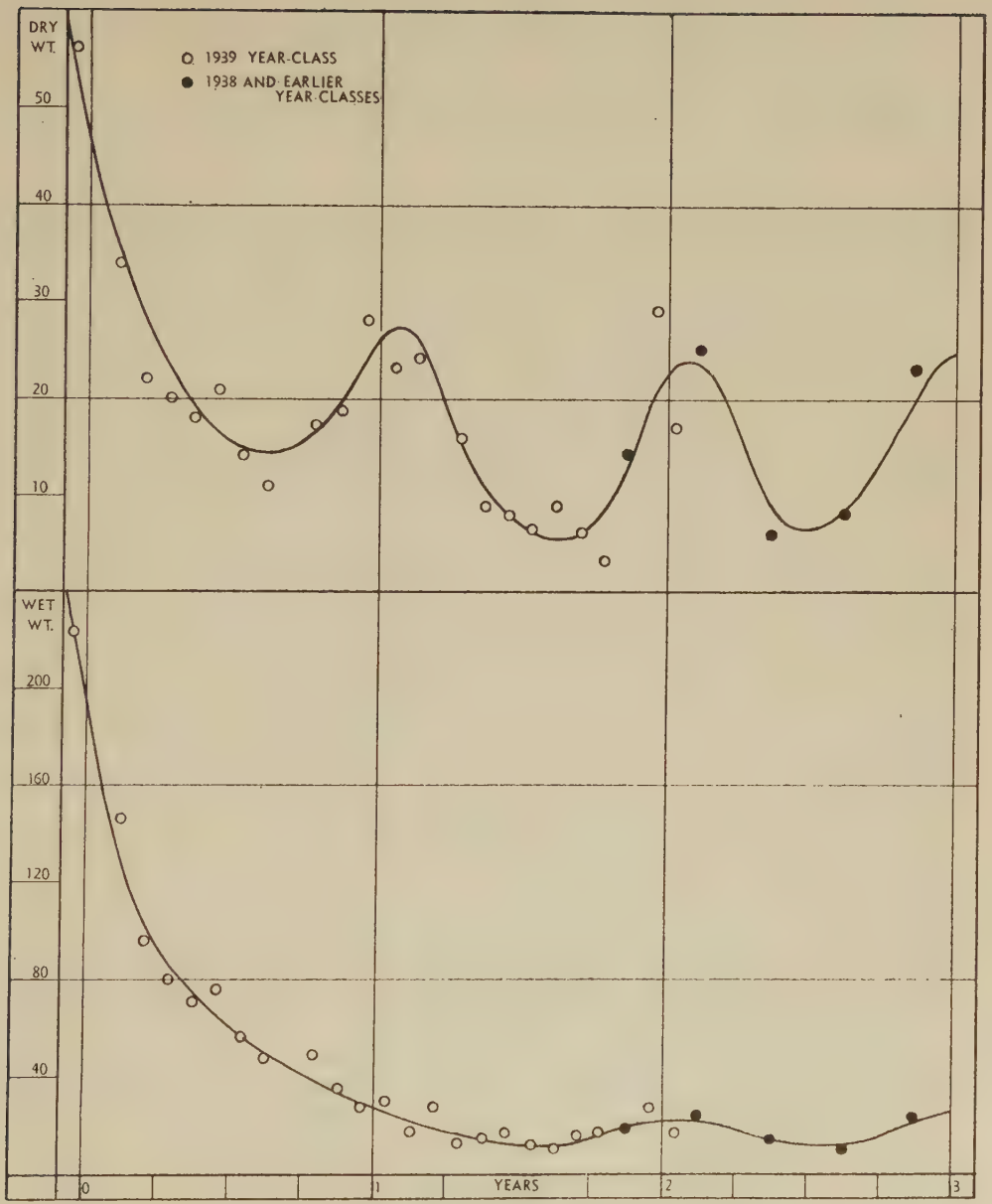

FIGURE 13. The variation in the amount of food in the stomachs of fish of the 1939, and the 1938 and earlier, year-classes; the dry and wet weights of food are both expressed as

$$10^4 \times \frac{\text{wt. of food}}{\text{wt. of fish}}$$

TABLE 51. The mean dry weight and estimated wet weight of the stomach contents of the fish of the 1938 and previous year-classes taken in each three-month period; results expressed in parts per 10,000 of the live weight of the fish.

	1940.		1941.		
	July–Sept.	Oct.–Dec.	Jan.–March.	Apr.–June.	July–Oct.
Number of fish ..	29	31	11	4	1
Dry weight	14	25	6	8	23
Wet weight	19	23	14	10	23

the periods when the trout are feeding predominantly on cased Trichoptera larvae. This suggests that these peaks are due to the presence in the stomachs of relatively large quantities of heavy indigestible mineral matter. For the purpose of studying the relation between food supply and the growth and production of the trout, the amount of utilizable food in the stomachs is of greater significance than is the total dry weight, which includes the mineral matter. An approximation of the utilizable food, which also permits direct comparisons to be made with data already set out for the bottom fauna, can be obtained by converting the dry weights into the wet weights of the actual living organisms without shells or cases, and the conversion factors given in Table 19 provide a means of doing this. To make the conversion, the contents of each stomach were considered individually, and a conversion factor was worked out according to the relative amounts of the different types of organisms present. Since the size range of each type in each stomach had been recorded, it was possible to make this estimate on the basis of relative bulks of the different types rather than on their relative numbers. The conversion factor determined in this way was then applied to the recorded dry weight of each stomach contents to give an approximate wet weight of actual organisms. The means of these wet weights are included in Tables 50 and 51 and plotted in Fig. 13. While the general trend is similar to that shown by the dry weights, the peak in the second summer has completely disappeared, and those in the later years are reduced to relatively small proportions. The wet-weight curve shows an obvious resemblance to the instantaneous growth rate curve which is plotted against the same time-scale in Fig. 9. This close correlation between amount of food in the stomachs and growth rate is similar to that which has elsewhere been shown to occur (Allen, 1941b) in the fresh-water stages of the Atlantic salmon, although the Horokiwi trout grow almost continuously, while the salmon showed strong seasonal changes. The dry weights of food found in the two species when growing at the same rate are also very similar, while the dry weights of food found in the stomachs of adult brown trout in Windermere in England (Allen, 1938) had monthly means ranging between 7 and 30 p.p. 10^4 which corresponds closely to the figures found for adult trout in the Horokiwi.

If conclusions are to be drawn as to the relation between the average amount of food in the stomachs and the total amount consumed in a day, it is necessary to determine whether there are any diurnal changes in the amount in the stomachs corresponding to daily feeding rhythms. The collections of fish were normally taken at any time between 9 a.m. and midnight according to the particular circumstances

of the day's work. The collections therefore represent a more or less random series of samples drawn from the various times of day and night between these limits. Since the time of capture of each fish was recorded, it is possible to determine the average amounts of food in fish taken in different parts of the day. From the results given earlier it is evident that the samples from all zones can be safely grouped, but that only a limited amount of seasonal grouping is permissible. In Table 52 therefore the mean estimated wet weight of food in 1939 year-class fish is shown for each three-hour period, the results being grouped for all zones into three-month intervals. No definite pattern is apparent in the results, and the

TABLE 52. The estimated wet weight of food in the stomachs of fish of the 1939 year-class in each three-hour period in which collections were made; results for each three-month period shown separately.

Period.		Time. 9.00–12.00.	12.00–15.00.	15.00–18.00.	18.00–21.00.	21.00–24.00.
Oct.–Dec., 1939	Number of fish	9	0	13	14	12
	Weight of food	126	..	124	154	139
Jan.–Mar., 1940	Number of fish	11	18	9	0	6
	Weight of food	108	69	46	..	79
Apr.–June, 1940	Number of fish	3	0	9	7	15
	Weight of food	37	..	54	70	49
July–Sept., 1940	Number of fish	14	17	21	6	5
	Weight of food	45	48	37	17	22
Oct.–Dec., 1940	Number of fish	16	27	19	0	0
	Weight of food	24	28	20	..	..
Jan.–Mar., 1941	Number of fish	15	20	20	7	1
	Weight of food	13	15	11	24	35
Apr.–June, 1941	Number of fish	7	8	7	4	1
	Weight of food	13	14	12	8	38
July–Sept., 1941	Number of fish	9	3	6	0	0
	Weight of food	33	16	17	..	..

fish are therefore probably feeding fairly uniformly during the day and that part of the night which was observed. The only experimental study of this problem which has been found is that of Hoar (1942) who examined the feeding pattern of young Atlantic salmon (*S. salar*) and brook trout (*Salvelinus fontinalis*). He found that these species normally fed steadily during the day, but usually took little food between 10 p.m. and 5 a.m., apparently as a result of habit or physiological rhythms rather than of environmental changes. He also found that at times an interruption of feeding occurred in the middle of the day; but this was apparently due to the occurrence of high temperatures, generally over about 20° C, at these times. We have already seen that such high temperatures are not usual in the Horokiwi, and this, together with the nature of the results actually obtained, makes it unlikely that a similar mid-day check in feeding occurs in the Horokiwi. On the other hand, the distribution of the collections during the 24 hours was such that a night check such as Hoar describes would not have been detected. Although

Hoar did not actually work with *S. trutta,* he found that this check occurred in two species closely related to it, and it therefore seems not improbable that it may also occur in the trout of the Horokiwi. If this is the case, the amounts of food recorded in the tables must be taken as those which correspond to a rate of feeding which would enable the fish to take the whole of their daily requirements in about two-thirds of each 24-hour period.

Apart from regular diurnal changes in feeding rate, there may also be irregular short-term changes due to environmental happenings. Cessation of feeding at high temperatures, as described by Hoar, would belong to this category, but we have already seen that this is probably unimportant in the Horokiwi. Increases in feeding rate due to temporary increases in the amount of easily accessible food might also be expected to occur. Such conditions might occur when a hatch of Ephemeroptera or Trichoptera is taking place and nymphs or pupae are drifting down in large numbers; and in times of flood, when both terrestrial and aquatic animals have been dislodged and are being washed downstream. The stomachs examined in the course of this work included a number which contained distinct masses of emerging Ephemeroptera nymphs which appeared to have been taken while a hatch of these forms was in progress. The total quantities of food in these stomachs did not however significantly exceed the normal for fish of that age at that season.

The effect of floods on feeding habits was not easily investigated, since netting could rarely be carried out under these conditions. A single opportunity did occur, however, in station R II on 29th October, 1940, when a small sample of fish was netted while the stream was still high and coloured after a minor flood. These fish, which consisted of four of the 1939 year-class, and one of the 1938 year-class, averaged 114 p.p. 10^4 estimated wet weight of stomach contents. By contrast, other fish taken in the same month contained an average of 30 p.p. 10^4 for the 1939 year-class, and 25 p.p. 10^4 for older fish. Determination of t for the comparison between composite samples of all age-groups taken under flood conditions, and on other days in the same month, gives a value of 5.51. This is twice the value for a probability of chance occurrence of 0.01, and there is therefore no doubt that, in this instance at any rate, fish which had been feeding under flood conditions contained quite abnormal quantities of food. Many more observations are needed to determine whether this is a normal occurrence, but the ease with which trout can often be caught on worms or similar baits on the bottom during a flood suggests that they feed very actively at these times.

In order to determine the degree of reliability of the estimates of the mean amount of food in the trout stomachs, the 95 per cent. fiduciary limits have been determined for the 10 monthly samples of the 1939 year-class which contained 20 or more fish. It was found that these limits ranged between $\pm$ 10 per cent. and $\pm$ 30 per cent. of the mean, with an average value of $\pm$ 22 per cent.; no regular trends in the range were apparent. In view of the consistency between the various samples in successive months, the actual fiduciary limits of the observations could safely be taken as being less than $\pm$ 20 per cent. of the observed values during the first year, and not very much greater even in later years, when the samples were generally smaller.

8. ANGLING RECORDS

(a) Objects and Methods

The previous sections have presented data regarding the number and size of trout which were produced in the Horokiwi during the period of the investigation. In order to determine the relation between this production and the quantity which the anglers were able to remove, it was necessary to collect as much data as possible regarding angling effort and catches in the Horokiwi. This was done mainly by the institution of the angling diary scheme already described. This scheme has been continued since the end of the other studies, and the results for the 10 seasons from 1939–40 to 1948–49 will be presented in this paper.

A total of 67 anglers have contributed at various times to the records, although the number in any one season has varied between 4 and 24. Since little supervision of the angling diaries was possible only approximate data regarding the sections of the stream in which fishing was done were usually available. For this reason, and because anglers often fished in two or more zones in a single outing, it is not possible to present separate angling data for each zone. It was found however that because of the heavily overgrown stretch of water at the junction of Zones II and III, and because of the position of the convenient access points, this junction was in fact a natural boundary for anglers, and with very few exceptions the records could be reliably allocated between the parts of the river above and below this point. It is fortunate that this boundary is probably also the most significant of the zonal boundaries in its relation to such factors as terrain, growth rate of trout, and composition of the bottom fauna. For convenience in discussing the results the two lowest zones will in future be jointly referred to as the "lower waters" and the three highest zones as the "upper waters."

While it is difficult to assess the completeness of the records obtained by means of the diary scheme, every effort was made to obtain information about this point, and an estimate was made in each season by the methods already discussed of the probable amount of fishing done, and number of fish caught, by unrecorded anglers. These amounts are included in the estimates of total fish and fishing effort. It is believed that the actual records for most seasons were about 90 per cent. complete. In many cases, however, the sizes of the individual fish were omitted from the returns, but there was a progressive improvement in this respect, and the proportion of the recorded fish for which sizes were given rose from between 30 per cent. and 40 per cent. for the first three seasons, until at the end it was generally between 70 and 100 per cent. The calculations on the size and age distribution of the total catch have been based on the assumption that these were the same for recorded and unrecorded fish taken under the same conditions.

(b) Total Fishing Effort and Crop

The main data on these matters are summarized in Table 53. It is apparent that the ten seasons may be divided into three groups according to the amount of angling effort which was expended in them. These changes can be linked closely with the influence of the recent war. War with Germany had begun shortly before the 1939–40 fishing season opened, but it had relatively little effect on angling

activity during the first year, and it is probable that the amount of fish removed was little if at all below that of pre-war seasons. The next two years saw only a gradual development of the war effort and a correspondingly slight reduction in the amount of angling. The outbreak of war with Japan in December, 1941, led to an abrupt intensification of the war effort, and by the 1941–42 season its effect on angling in the Horokiwi had become very marked. The angling effort fell to about an eighth of the pre-war level and remained at the same low intensity for the 1943–44 and 1944–45 seasons. In August, 1945, war came to an end and conditions generally began to revert to normal; correspondingly the amount of angling in the Horokiwi rose abruptly in the following season, and afterwards oscillated about the new level. This new level is noticeably below that of the first three seasons; the difference is due mainly to the absence of certain week-end residents of the Horokiwi valley who had fished the stream very regularly in earlier years; if these local anglers are neglected, the average total number of hours per season is the same, at 270, for the first three seasons, and for the last four.

Two of the most direct ways in which the war influenced the amount of angling were the withdrawal of anglers for service in the armed forces, and the restriction of travel, particularly by petrol rationing. As an indication of the influence of recruitment on angling in the Wellington district as a whole, Table 53 shows the licence revenue received by the Wellington Acclimatization Society in each of the ten seasons. Actual numbers of licences issued are not available, but there were no changes in licence rates during the period, and changes in the proportion of the various types of licence were probably small; the changes in revenue do therefore give quite a good indication of the changes in numbers of licences sold from season to season. Licence revenue shows variation which is very different from that shown by the Horokiwi angling effort, and which cannot be correlated so closely with the obvious war-time effects; apart from a temporary drop in 1941–42, the decline does not commence until 1943–44 but then it continues until 1946–47; the abrupt rise does not occur until 1947–48, two years after the war ended and one year after the rise in Horokiwi angling. The local effects on the Horokiwi therefore do not seem likely to have been due, to any great extent, to the direct effects of recruitment.

On the other hand, the position of the Horokiwi is such that angling there is particularly susceptible to variations in the availability of petrol. The nearest permanent homes of anglers known to fish the Horokiwi were at Plimmerton, about three miles from the nearest part of the stream, while the great majority lived in the major residential areas of Wellington and the Hutt Valley, about 20 miles away. The nearest railway station is at Plimmerton, and no bus routes of any value pass any nearer to the valley, and it is therefore practically essential for any angler fishing the Horokiwi to possess private means of transport. A few young anglers visit the stream on bicycles, but well over 90 per cent. of the Horokiwi anglers travel by private motor-car, and it is this which makes the effects of petrol rationing so pronounced. These effects are clearly shown in Table 53 in which the amount of angling in each season is compared with the amount of petrol available. The amount of petrol is expressed in terms of the number of standard coupons which could be redeemed during the fishing season; the value

TABLE 53. The main data on angling effort and results for the seasons between 1939-40 and 1948-49 for both lower and upper waters, and for the whole stream; also the amount of petrol available to anglers during each season in terms of a standard coupon; F denotes that the petrol was unrationed during the whole or the major part of the season; also angling licence revenue received by the Wellington Acclimatization Society during each season.

	Lower Waters.							Upper Waters.							Combined.								
Season.	Days.	Hours.	Fish Killed.	Total Weight (lb.).	Mean Weight (lb.).	Catch Per Hour.	Under-sized Per Hour.	Days.	Hours.	Fish Killed.	Total Weight (lb.)	Mean Weight (lb.)	Catch Per Hour.	Under-sized Per Hour.	Days.	Hours.	Fish Killed.	Total Weight (lb.)	Mean Weight (lb.)	Catch Per Hour.	Under-sized Per Hour.	Petrol Avail-able.	Angling Revenue £
1939-40 ..	c. 150	533	334	296	0·93	0·63	0·41	5	12	21	16	0·77	1·83	1·30	c. 155	545	355	312	0·89	0·63	0·43	F.	1,762
1940-41 ..	124	466	275	244	0·92	0·61	0·70	5	12	15	11	0·80	1·27	2·80	129	478	290	255	0·91	0·62	0·76	17	1,752
1941-42 ..	92	329	193	185	0·96	0·65	0·91	15	53	43	35	0·82	0·84	1·37	107	382	236	220	0·86	0·68	0·98	6	1,518
1942-43 ..	20	64	28	32	0·96	0·49	0·23	1	2	1	1	0·85	0·67	0	21	66	29	33	0·89	0·50	0·22	4½	1,792
1943-44 ..	13½	61	19	16	0·83	0·44	0·65	14½	77	43	39	0·91	0·56	1·26	28	138	62	55	0·90	0·54	1·09	4½	1,534
1944-45 ..	21	60	34	34	1·03	0·57	1·31	8	32	26	20	0·75	0·80	0·65	29	92	60	54	0·86	0·67	0·87	4½	1,324
1945-46 ..	57	375	143	124	0·90	0·48	0·64	10	36	24	19	0·89	0·67	0·93	67	411	167	143	0·90	0·50	0·66	14	1,265
1946-47 ..	113	251	105	109	1·05	0·49	0·29	14	45	18	14	0·76	0·51	1·65	127	296	123	123	0·98	0·49	0·52	F.	1,260
1947-48 ..	37½	124	60	55	0·93	0·50	1·05	10½	24	22	18	0·80	1·05	2·78	48	148	82	72	0·89	0·61	1·38	F.	1,910
1948-49 ..	70	179	107	98	0·93	0·68	1·05	18	43	46	36	0·77	1·27	1·44	88	225	153	134	0·87	0·83	1·14	24	1,946
Total	698	2,442	1,298	1,193	0·96	0·58	0·66	101	336	259	209	0·81	0·83	1·42	799	2,781	1,557	1,401	0·91	0·61	0·76	..	..

of a coupon varied according to the size of the car for which it was issued, and was three gallons for medium-sized cars, and correspondingly more or less for larger and smaller cars. The amount of fishing in the Horokiwi usually followed closely the variations in the amount of petrol available. The fact that fishing continued at a substantial rate in 1941–42 although the amount of petrol was greatly reduced was probably due to two main causes; first, the real intensification of rationing did not begin until December, 1941, after the two most important angling months on the Horokiwi were past; secondly, the week-end residents mentioned earlier were still fishing the Horokiwi, and probably were prepared to devote an unusually high proportion of their available petrol to that purpose.

The unusual amount of angling recorded from the upper waters in 1941–42 and 1943–44 was due to the presence of a single angler who fished this part of the stream both hard and skilfully for those two seasons, and subsequently left the district.

(c) Size of Fish

During the whole period studied the minimum size limit fixed by the regulations remained unchanged at 11 inches. The average weights recorded for the various seasons are therefore truly comparable, as they represent the average weight of all fish caught which exceeded the minimum size. A few takeable fish were returned, but these formed a negligible proportion of the whole catch. In Table 53 the data are expressed as average and total weights, but anglers were actually asked to record lengths of fish rather than weights, because it was believed that more accurate returns would be obtained in this way. The instruments used for measuring length—rules and tape-measures—do not usually develop with age the errors which are so frequent in the spring-balances used by most anglers for weighing fish. It was also felt that those few anglers who are content to give estimated data rather than actual measurements would probably provide more accurate lengths than weights. The individual length measurements were converted into corresponding weights using a condition factor of 120, which has already been shown to be a typical value for Horokiwi trout of takeable size. The data presented in Table 53 have been derived from these computed weights.

The average weight of fish taken by anglers in the lower waters has remained very uniform throughout the period of the observations. The only season in which the mean weight of an adequate sample of fish diverged appreciably from the normal was 1946–47, when, for some reason, the fish were of unusually large average size. The data for the upper waters are less regular; the variations probably arise from two causes, the smaller size of the samples, and the greater diversity of the populations from which the fish were taken. Although, as has been shown earlier, there are some differences in growth rate and ultimate size between Zones I and II, which together form the lower waters, they are not as great as those between the three zones of the upper waters. It is evident however that, except in 1943–44, when the lower water sample was very small, the average size was always lower, and generally much lower in the upper waters than it was in the lower waters.

(d) Angling Catch by Year-class

The proportion of the fish in each season's catch which was drawn from each age-group can be estimated from the data concerning the sizes of fish caught by anglers, and the growth rates of trout in the Horokiwi. The accuracy of these estimates is greatly assisted by the distinct size ranges of the fish of the younger age-groups in the Horokiwi. Owing to the rapid growth rate, it was necessary to allocate the recorded fish to year-classes month by month instead of making a single allocation for the whole season. To make the allocation, all fish recorded in each season were entered on a squared table having length on the vertical axis and months of the angling season along the horizontal axis. This table was then divided into regions belonging to different age-groups by inserting boundary lines derived from the size distribution and growth data of the 1939 and 1940 year-classes. For all seasons except 1941–42 and 1942–3 standard boundary lines derived from the growth of fish during 1940 were used. For these two seasons, when a significant part of the catch had been adversely affected by the 1941 floods, special lines derived from the 1941 growth curves were used. In the lower waters, the standard boundary between age-groups I and II was taken to be just below 11 inches at the beginning of the season, and to rise at a decreasing rate to 12.3 inches at the end of the season; the boundary between age-groups II and III was taken to rise during the season from 12.8 inches to 16.0 inches, and that between age-groups III and IV was taken to be constant at 16.5 inches; the very small proportion of fish older than age-group IV, which were present in the anglers' catches, was included in this group.

TABLE 54. The number of fish allocated to each age-group in each part of each season, and the mean and standardized percentage composition of the fish caught in each part of each season; results for the lower waters only.

Age-group.	I.			II.			III.			IV.		
Season.	Oct.–Nov.	Dec.–Feb.	Mar.–Apr.	Oct.–Nov.	Dec.–Feb.	Mar.–Apr.	Oct.–Nov.	Dec.–Feb.	Mar.–Apr.	Oct.–Nov.	Dec.–Feb.	Mar.–Apr.
1939–40 ..	5	10	5	38	9	3	8	3	0	1	1	0
1940–41 ..	4	14	9	33	8	3	16	1	0	2	0	0
1941–42 ..	0	1	7	18	4	17	10	0	1	1	1	0
1942–43 ..	0	..	..	7	..	..	8	..	..	1	..	..
1943–44 ..	0	..	..	8	..	..	1	..	..	0	..	..
1944–45 ..	0	0	0	5	1	1	1	0	0	1	0	0
1945–46 ..	1	10	1	21	13	6	5	0	0	0	0	0
1946–47 ..	1	7	1	20	1	1	14	1	0	4	0	0
1947–48 ..	3	3	..	31	0	..	9	0	..	2	0	..
1948–49 ..	0	5	4	48	5	0	16	0	0	1	0	0
Mean percentage	5	53	59	68	40	41	23	5	0	4	1	0
Standard percentage ..	5	50	60	70	44	36	22	5	4	3	1	0

Since the proportions in which the different age-groups were captured changed so much during the season, the season was divided into three periods, i.e., October to November, December to February, and March to April. Table 54 shows the number of fish taken in the lower waters which were allocated in this way to each age-group during each period of each season; the table of course only includes those fish for which individual lengths were recorded. From these figures the average age-composition of the fish caught in each period of each season has been determined, and in the final line some standardized percentages obtained by

smoothing out obvious sampling irregularities are set out; the results for the 1941–42 and 1942–43 seasons were omitted in obtaining the mean and standardized percentages as these seasons were affected by the 1941 floods. These standardized percentages were then applied to the total numbers of fish estimated to have been taken in each period of each season, and the combined results are set out in Table 55 as the estimated total number of each year-class captured in each season. This procedure was adopted because sampling errors sometimes led to considerable variation in the age distribution from season to season, particularly

TABLE 55. The estimated number of fish of each year-class taken in the lower waters of the Horokiwi in each season. An asterisk indicates that the year-class was not completely cropped within the period studied.

Season.	Year-class. 1935.	1936.	1937.	1938.	1939.	1940.	1941.	1942.	1943.	1944.	1945.	1946.	1947.
1939–40 ..	6	44	185	99	..	..	..	..	..	..	..	..	..
1940–41 ..	..	5	36	153	81	..	..	..	..	..	..	..	..
1941–42 ..	..	..	14	26	113	22	..	..	..	..	..	..	..
1942–43 ..	..	..	..	1	12	12	3	..	..	..	..	..	..
1943–44 ..	..	..	..	..	0	3	12	4	..	..	..	..	..
1944–45 ..	..	..	..	..	..	0	4	19	11	..	..	..	..
1945–46 ..	..	..	..	..	..	..	3	15	73	52	..	..	..
1946–47 ..	..	..	..	..	..	..	..	2	14	58	30	..	..
1947–48 ..	..	..	..	..	..	..	..	..	2	12	40	6	..
1948–49 ..	..	..	..	..	..	..	..	..	..	3	20	69	15
Total ..	6*	49*	235*	279	206	37	22	40	100	125	90*	75*	15*

when the numbers of fish measured were small, and it was therefore believed that more accurate results could be obtained by applying the standardized percentage compositions derived from the much larger combined samples based on all the normal seasons. The fish caught in the 1941–42 and 1942–43 seasons were allocated by the same methods, but the special boundary lines derived from the growth rates of the year-classes concerned were used. The extent to which the various year-classes have been cropped by anglers has obviously depended mainly on the variations in intensity of angling effort. In the lower waters each year-class is cropped most heavily in its second and third years, and the relative proportions taken in each of these seasons depend largely on the extent to which the stream is fished in the autumn of the second year, since the proportion of takeable fish in the year-class is rapidly increasing at that time. The Horokiwi is normally not fished as heavily in the autumn as in the spring, and consequently a year-class yields the greatest number of fish to anglers while in its third year.

A similar technique has been applied to the much smaller numbers of fish taken in the upper waters. The typical growth rate is so much less in this part of the stream than in the lower waters that the fish are approximately a year older before

TABLE 56. The number and percentage of fish caught in the upper waters which were allocated to each age-group.

	Age-group II. Oct.–Nov.	II. Dec.–Feb.	II. Mar.–Apr.	III. Oct.–Nov.	III. Dec.–Feb.	III. Mar.–Apr.	IV. Oct.–Nov.	IV. Dec.–Feb.	IV. Mar.–Apr.
Number	10	26	12	96	47	1	16	9	1
Percentage	8	32	86	79	57	7	13	11	7

they begin to reach takeable size. The boundary line between age-groups II and III was taken as running directly from 11.0 inches at the beginning of the season to 12.5 inches at the end, while that between age-groups III and IV changed from 13.0 to 14.0 inches during the season. Table 56 shows the total numbers for all seasons and the percentages of fish caught in each period which have been allocated to each age-group. Using these mean percentages, the fish caught in each season have been allocated to the respective year-classes with the results given in Table 57. The rather erratic fluctuations which appear are largely due to the variations in the amount of angling in this part of the stream. It appears that in these waters cropping is substantially concentrated on the fish in their fourth year, so that most of the fish taken by anglers are older, although smaller, than those taken in the lower waters.

TABLE 57. The estimated numbers of fish of each year-class in the upper waters of the Horokiwi in each season. An asterisk (*) indicates that the year-class was not completely cropped within the period studied.

Season.	Year-class. 1935.	1936.	1937.	1938.	1939.	1940.	1941.	1942.	1943.	1944.	1945.	1946.
1939–40	5	13	3	..	..	..	..	..	..	..	..	..
1940–41	..	4	9	2	..	..	..	..	..	..	..	..
1941–42	..	..	9	29	5	..	..	..	..	..	..	..
1942–43	..	..	..	0	1	0	..	..	..	..	..	..
1943–44	..	..	..	..	9	29	5	..	..	..	..	..
1944–45	..	..	..	..	..	7	17	2	..	..	..	..
1945–46	..	..	..	..	..	..	5	16	2	..	..	..
1946–47	..	..	..	..	..	..	..	5	12	1	..	..
1947–48	..	..	..	..	..	..	..	..	3	17	2	..
1948–49	..	..	..	..	..	..	..	..	..	12	29	5
Total	5*	17*	21	31	15	36	27	23	17	30	31*	5*

(e) Rate of Catch

The rate of catch as measured by the average number of takeable fish caught per hour's fishing provides a useful index of the quantity of fish present from the point of view of the angler. The annual mean rates of catch for the two main divisions of the Horokiwi are shown in Table 53. In the lower waters this has varied rather erratically between limits of 0.44 and 0.68 fish per hour, while in the upper waters it has ranged between 0.51 and 1.83. A considerable quantity of data regarding rates of catch in trout waters in all parts of New Zealand has been collected in recent years by means of a widespread angling diary scheme, and it appears that the great majority of trout waters give rates of catch ranging between 0.4 and 1.20 fish per hour. The rates in the lower waters of the Horokiwi thus lie within the lower part of the normal range, while the upper waters have, at least in the best years, given rates of catch which are distinctly good. The most marked change in the lower waters occurred in 1942–43 when the rate, which had been consistently above 0.6, suddenly dropped to 0.49, and to an even lower level in the following year. After this minimum it continued to vary about a slightly higher level, until it rose abruptly again in 1948–49. The year-classes which would usually have provided the bulk of the catch in 1942–43 and 1943–44, when the rate of catch first decreased, were those of 1940 and 1941. It has already been shown that both these year-classes suffered severely in the floods of 1941, the 1940 year-class through the reduction of the yearling population, as is shown in Table 30, and the 1941 year-class through the destruction of redds. The con-

tinued low levels were probably due at least in part to the fact that the year-classes concerned would have been largely the descendants of the 1940 and 1941 year-classes. The rise in 1948–49 may have been due to the natural process of recovery, although it was remarkably sudden. It is interesting to note that this apparent scarcity of the 1941 year-class occurred despite the fact that in that year the number of fry liberated in the Horokiwi was 30,000, which was the highest number since 1935, and three times as many as in any of the preceding three years.

In the upper waters the rate of catch showed even more pronounced fluctuations. It dropped steadily from a very high value in 1939–40 to a minimum in 1943–44, and then after minor irregular movements for three years rose again sharply in the last two seasons studied. The general trends of these movements are rather similar to those of the lower waters. That the similarity in the fluctuations in rate of catch in the two parts of the stream has some significance, and is due to the influence of the same factors, is indicated by the fact that the correlation coefficient r for the two series is 0.697, which is well above the value for 95 per cent. probability. Since anglers' reports had suggested that fishing of the upper waters was a fairly recent development in 1939–40 it appeared possible at first that the pronounced decrease in the rate of catch in this area between 1939 and 1944 was due to the depletion of the limited population of takeable fish in these small waters. Since that time, however, a pronounced rise in the rate of catch has occurred between 1946 and 1949, although more fish were being removed in each season than in the period of decreasing rate of catch.

The average rate of catch of under-sized fish is usually greater than that of takeable fish in both parts of the stream, although it tends to fluctuate rather more erratically. In the upper waters the general pattern over the ten-year period is very similar to that shown by the takeable fish. This could however occur whether the fluctuations were due to variations in the abundance of the population or to the influence of such factors as weather conditions and anglers' skill. The fact that the correlation coefficient r between the rate of catch of takeable fish in one season, and that of under-sized fish in the previous season is twice as great (0.52) as that between takeable and under-sized fish in the same season (0.26) suggests that the abundance of the stock played an important part in determining the rate of catch. In the lower waters no correlation approaching significant levels can be found between the rates of catch for takeable and under-sized fish.

The only change in the angling regulations which might have affected the rate of catch during the period studied was the prohibition in 1941 of the use of any lure or bait other than artificial fly on the Horokiwi. Observations in the two seasons prior to this prohibition suggested however that other methods were so rarely used in this stream that the change is not likely to have had any significant effect on the average rate of catch.

In the Horokiwi, as in the rest of the Wellington Acclimatization district, a bag limit of twelve fish per day has been in force during the whole of the period studied. The records of the ten seasons included details of 455 daily bags, which included only three limit bags, one in 1939–40, and two in 1940–41. It is evident therefore that this regulation has had, at least since 1939, a negligible effect on

the quantity of fish taken from the Horokiwi. In the seven seasons examined since 1942 only one bag of more than eight fish has been recorded.

The reliability of the estimates of angling catch cannot be examined by the methods which were used in previous sections of this report. This is because those sections dealt with accurately measured small samples of the material under study, which could be subjected to statistical analysis, whereas in the present section we have been concerned with data which are believed to be relatively complete, but in which the accuracy of the measurements is sometimes uncertain. The errors in this part of the investigation are therefore generally not due to sampling, and so are not susceptible to statistical analysis. Many anglers, particularly among those who fished the Horokiwi regularly, took a great deal of trouble to ensure that the diaries which they sent in were complete and accurate. Some other records were however either incomplete or approximate; in particular, the length of time fished, and the numbers of under-sized trout caught, were not infrequently omitted, while the sizes of takeable fish were not always in a form which allowed them to be combined with the rest of the data. In such cases allowance had to be made for the incomplete returns by the use of mean values derived from the complete records. Since the proportion of complete records was fairly high in most seasons, it seems unlikely that the estimates are generally in error by more than 10 per cent., except in the 1939–40 season, when the scheme was in its infancy.

9. SUMMARY

Data were collected by netting trout at regular intervals mainly at six standard stations; for quantitative purposes these stations were covered thoroughly at quarterly intervals, and a special netting of half the stream in alternate sections was also carried out in May, 1941. Estimates of egg and fry production were supplemented by the regular counting of all visible redds and by the excavation of a sample series.

There is little or no interchange of trout between the Horokiwi and other waters, and within the stream itself there is relatively little movement. It is estimated that only about 20 per cent. of the fish moved out of a station in three months, and that only 20 per cent. of those remaining had moved more than 250 ft. There was no significant spawning migration.

Estimates of the population of each station were based on the mean efficiency of netting (15 per cent.) and on the number of fish caught in the routine nettings. These were extended to give the zonal populations by using the results of the more thorough netting of May, 1941. The estimates obtained are given in Table 30. The 95 per cent. confidence limits of these estimates are believed to be about $\pm$ 50 per cent. at the best.

The main estimates of egg production were based on the estimates of the number of mature females in each year-class in each zone, and the determination of the relation between size and individual egg production. The sexes were evenly divided, and 91 per cent. of females matured in their second year, and nearly all the remainder in their third year. Egg production was linearly related to length by the expression $N = 61.24\ (L - 15.65)$ where N is the number of eggs and

L the fork-length in cm. In both 1940 and 1941 egg production was about 888,0000 with 95 per cent. confidence limits of ± 50 per cent.; losses due to incomplete spawning and failure of eggs to lodge were probably negligible; losses due to disturbance by later spawners were not more than 10 per cent.; a few redds were accidentally destroyed by man; destruction by floods was negligible in 1940 but may have amounted to 80–90 per cent. in 1941.

The mortality rate was very high at first, but decreased rapidly, and during the later part of the first year was fairly steady with an instantaneous daily value of 0.00349. It afterwards increased again and seemed to be constant in the later years with a mean value of about 0.00486. The time of increase in mortality rate coincided approximately with the first spawning and the beginning of exploitation by anglers.

Growth studies were based on the frequent measurement of samples of fish from all available year-classes. The year-classes were identified by their size distribution up to about the end of the second year, and by scale reading thereafter. Growth varied considerably in different parts of the stream, being most rapid in Zone I, becoming progressively slower up to Zone IV, and increasing in rate again in Zone V. The approximate sizes at the end of the first and second year were 22 cm. and 31 cm. in Zone II, and 18 cm. and 24.5 cm. in Zone IV; after the second year the rate of growth was relatively slight. These rates are very much greater than those obtained in previous scale-reading studies of other New Zealand waters, and it is suggested that this may be due to the frequent inclusion of a false first-winter band in the earlier scale readings. Growth in weight generally follows a Minot curve until the middle of the second summer and gives a reasonably good fit to an equation of the form $\log W = k_0 + k_1 \log (t - n)$; after the second summer the growth rate decreases more rapidly and can be fitted to an equation of the form $W = A - B e^{-kt}$ as suggested by Brody for the upper half of the sigmoid growth curve. The 95 per cent. confidence limits in the estimation of mean weights are generally about ± 5 per cent. The floods of 1941 caused significant checks in the growth of the 1939 and 1940 year-classes.

The normal condition factor fell from 130–120 in the first year to 120–110 in later years. Condition was also adversely affected by the floods of 1941.

Food studies were based on the stomach contents of samples of fish taken in most zones generally at monthly intervals. The contents were recorded both numerically and by weights; the dry weights were determined directly and the wet weights computed from them. The main source of food was the bottom fauna, but not more than 5 per cent. was taken at the surface, and in the older trout not more than 20 per cent. by weight, or 0.1 per cent. by number, of the food consisted of small native fish. The forage ratios of all the main constituents of the bottom fauna have been examined and were found to fall into three groups, with high, medium, and low to zero ratios. The forage ratios generally conformed to the usual pattern and were higher for the animals with habits which made them conspicuous, while they increased with the size of the trout for forms with hard shells or cases, and decreased for soft-bodied forms.

The only animals which formed an important part of the food all fell in the high group and comprised *Deleatidium* nymphs and four Trichoptera larvae,

Olinga, Helicopsyche, Pycnocentrodes, and Sericostomatid type "C," which together generally made up 85 per cent. to 95 per cent. of the food. *Delcatidium* had a high ratio for young trout; *Helicopsyche, Pycnocentrodes,* and Sericostomatid type "C" had a low ratio for first-year trout and thereafter showed seasonal fluctuations, the ratio only being high when the larvae were large; *Olinga,* which has large larvae present at all seasons, had a consistently high ratio for trout after the first year.

There were no signs of changes in the composition of the food according to the number of animals in the stomach.

The wet weight of food in the stomachs decreased rapidly in relation to the weight of the fish during the first year and more slowly thereafter, and followed a very similar curve to the instantaneous growth rate. The relative dry weight followed a similar curve with subsidiary peaks in the later summers caused by the cases and mineral shells then present in the food. The amount of food in the stomachs showed no diurnal variations. The 95 per cent. confidence limits of the estimates of amount of food in stomachs are about ± 20 per cent.

Fairly complete data of angling catches were obtained by means of a voluntary diary scheme. The amount of fishing effort fell from about 500 hours per season in 1939 to 1942, to about 100 hours in 1942 to 1945, and then rose again to about 200 to 400 hours. The variation was controlled largely by the amount of petrol available to anglers. The number of fish caught showed parallel variations. The average weight of the fish taken by anglers was generally about 0.95 lb. in the lower waters, and 0.8 lb. in the upper waters. In the lower waters most fish were taken from a year-class in its third year, and in the upper waters in its fourth year. The average rate of catch in the lower waters was rather over 0.6 fish per hour from 1939 to 1942; it then dropped suddenly to about 0.5 and remained at this level until 1948, when it rose abruptly to the previous level. In the upper waters somewhat similar changes occurred, but the rate of catch was generally higher. It is believed that the period of low rate of catch was due, at least in part, to the reduction of the population by the 1941 floods.

PART V

Discussion

1. THE NATURE OF PRODUCTION

The study of productivity in the fresh-water community has been approached by many workers, from a variety of angles, and with very inconsistent terminologies. In particular, there has been a noticeable division between the approach of the limnologist, who is concerned with the entire biological community of the water studied, but who, on account of the very complexity of his problem, is unable to study any one trophic level in any great detail; and that of the fisheries worker, who is concerned only with one group, and often only one species in the community, but who, on account of the greater detail of the studies made on the selected group, is often unable to consider its relation to the remainder of the community. Understanding of the productivity phenomena in any community is dependent on a knowledge of the food relationships between the component organisms. In fresh waters these studies, the development of which has been reviewed by Lindeman (1941), led first to the construction of food-chains, and later to the successional concepts developed for lakes by Thienemann and others. As techniques were developed for the measurement, even approximately, of the quantities involved, it became possible to place the theoretical analysis of these relationships on a more secure footing, and to begin to build up a mathematical theory. While most of the quantitative studies have been confined to one or two levels in the food-chain, a few attempts at the quantitative assessment of the entire structure have been made; this has been done for small lakes by Juday (1940) and Lindeman (1941), while, in a marine area, Harvey (1950) has recently surveyed the available data regarding production at all levels in the western part of the English Channel. Lindeman (1942) has examined the structure of a typical lake community, and shown both on theoretical grounds and by the application of available data from several sources that the Eltonian pyramid is a necessary feature of the structure of a community which consists of several trophic levels. More recently Macfadyen (1948), in a very useful review, has drawn attention to the confusion which has arisen from the varying terminologies used by different workers, and has tried to establish the true synonymies; he has also emphasized the necessity of distinguishing clearly between the energy and matter cycles, and has pointed out that while the energy cycle is essentially single, a great degree of re-circulation of matter can occur, since the matter serves primarily as a vehicle for the conveyance of energy.

The biological community inhabiting a stream such as the Horokiwi is fairly close to the ideal simple case:—

Inorganic Materials ——> Plants ——> Herbivores ——> Carnivores

The plants of the stream itself are mostly algae, and particularly diatoms, although higher plants may be locally important along the margins. A second contribution to this trophic level is made by the detritus, produced by the breakdown of terrestrial plants of the drainage area, which is washed into the stream.

The herbivores in such a community are mainly the invertebrates of the bottom fauna—insecta, mollusca, crustacea, etc.

The principal carnivores are the fish.

Complexities in the chain arise mainly in two ways. Re-circulation of matter occurs through the breakdown and re-utilization of dead individuals of all levels, and partial extra levels are introduced both by the fact that some of the insects eaten by the fish, e.g., *Archicauliodes* and some Rhyacophilidae, are themselves predatory on smaller invertebrates, and by the appearance among the food of the large trout of some small fish which are themselves primary predators. The long-finned eel is mainly a secondary predator when large.

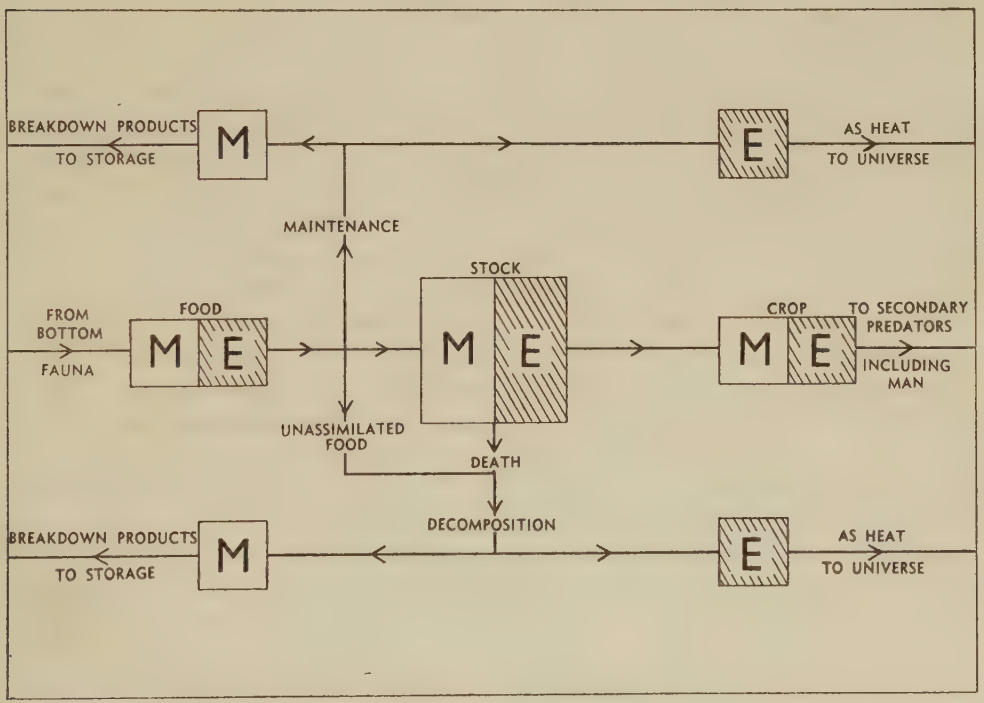

FIGURE 14. A section of a food-chain centred on a predator such as the trout, showing the paths taken by energy (E) and matter (M).

Although it becomes a secondary predator when it eats small fish or predatory insects, the trout may, for simplicity, be regarded as forming a portion of the primary carnivore level in the community, and as such its relations with the rest of the community may be summarized in Fig. 14, which represents in simplified form the matter and energy relationships of any of the higher levels in the food-chain. Food is ingested from one or more lower stages in the form of matter in

which a certain quantity of energy is stored. Most of the food is assimilated but a certain amount passes through the fish and is defecated; this part of the matter, and the energy stored in it, has been removed from the lower levels of the chain by the action of the fish, but has not been used by them in any way. Of the food which is assimilated, part is immediately used to provide energy for maintenance and activity, and part is used in the growth of the fish. The matter in the part used for maintenance is broken down, and the breakdown products are passed back into the system by respiration and excretion and so become available for re-circulation. The energy is converted into heat and passes out into the surrounding medium; as Macfadyen has pointed out, this energy is now lost to the system, and, unlike the matter, cannot be re-circulated. The food used in growth is in part incorporated in changed form in the body of the fish, and in part excreted as waste products of the change. The energy which has been released during these changes is transferred to the environment in the form of heat. Some energy is still contained in the organic waste products which are excreted as a result of both maintenance and growth. Some of this energy may be re-circulated by the direct utilization of these substances by bacteria and other organisms but most of it is probably released by the processes of decomposition.

The additional matter which has been incorporated in the bodies of the trout as a result of these changes is the amount of new trout material which has been produced. At the same time some of the material already incorporated in the trout is being withdrawn and transferred to other levels in the chain. A major part of this conversion is caused by the predators at higher levels, including man, which draw their food supplies from the trout. The cycle which has been described above occurs again at this higher level, but since some of the predators concerned, such as man and fish-eating birds, may live outside the water system so far considered, the return even of the matter to the system becomes uncertain. The remainder of the conversion takes place through the death of trout from causes such as disease, old age, and accident, which do not automatically involve their ingestion by another animal. The bodies of these trout, like the non-assimilated matter referred to above, may be broken down through the action of scavenging and decomposing organisms of various kinds. The material products of this breakdown remain in the system and are available for re-circulation, while most of the energy which was stored in the material is released to the environment in the form of heat and lost to the system. Some of the scavenging and decomposing organisms may however be eaten by predators of various levels, and a part of the matter of their bodies will be incorporated in the bodies of the predators. The energy incorporated in this material is also carried to the predator level for a second time; this would appear to be the principal exception to the rule laid down by Macfadyen that energy is never re-circulated. It must be emphasized however that this re-circulating energy is not being used, but is simply being transported in the material of the bodies of the various organisms concerned. Once it has been used in maintaining the activity of any organism it is converted into heat and lost to the system.

The population or stock of trout, or of any other organism, can therefore be regarded as being in a perpetually changing state of balance between the new

material which has been incorporated in it by the processes of growth, and the material which has been lost by mortality and emigration. This balance exists whether the energy cycle or the matter cycle is being considered, and indeed when attention is restricted to a single level of the chain the essential difference between these cycles, which is of great significance over the ecosystem as a whole, becomes relatively unimportant. When this balance is considered quantitatively the inconsistency between the terms employed by different workers becomes apparent. The energy contained in the food taken into any level is called the "productivity" of that level by Lindeman (1942) and Hutchinson (1942), although it is not clear whether this includes the energy contained in the non-assimilated food. Of the assimilated food, part is directly utilized in the maintenance of bodily activity. The "maintenance ration" of Dawes (1930, 1931), Pentelow (1939) and Ricker (1949a) refers to the quantity of food required to maintain a fish at constant weight without allowing any growth; the "food used for keeping up body and energy" of Karzinkin (1939) on the other hand is the total weight of assimilated food, less the increase in weight of the fish. The energy released as heat in any level is described by Macfadyen (1948) as the "activity" of that level. The amount of additional trout material which is formed by conversion of the food has been described as "production" by many workers, Borutzky (1939a), Allen (1946), Clarke (1946), Ricker (1946); but as "yield" by Macfadyen (1948). The quantity passing on to the next level has also been variously described; its energy content is the "productivity" of the next level of Lindeman and Hutchinson, and the amount of matter passing to one particular organism at the next level has been described as the "crop" (Allen, 1946); "yield" (Ricker, 1946, and Rounsefell, 1946); "production" (Needham, 1940). The amount of trout material existing at any one time is the difference between the amount produced up to that time and losses due to predation by higher levels in the chain, and to mortality from disease, accident, etc. This quantity has also been variously described, and is the "stock" of Allen (1946); the "standing crop" of Ricker (1946); the "biomass" of Borutzky (1939a); and has also been called "production" by some workers.

In the above discussion no distinction has been made between the actual quantities involved and their associated rates, although, as Macfadyen has pointed out, some workers have used different terms for the two measurements. A measurement of any of these quantities must obviously refer to a fixed and, generally, a defined period of time, and must therefore involve the determination of, at least, the mean rate over that period.

The three quantities, and associated rates, which are most conveniently determined for any species or group of species which forms a single level in the chain, are the quantity of matter incorporated into the species within the period, the amount of matter existing in the species at a particular time, and the quantity of matter of that species consumed by the organisms of a higher level within the period. The importance of distinguishing clearly between these three quantities was stressed in the preliminary report on the present work (Allen, 1946), and the terms then used were "production," "stock," and "crop" respectively. These terms will be used in the same sense in this report, although the use of "production" in this sense has been objected to (Macfadyen, 1948) on account of the variety of

other meanings which have been attached to it; it has however been used in this sense by most of the workers who have attempted to estimate this quantity, and the only alternative proposed, "yield," has also been used in a different sense by Ricker (1946). The other two terms do not appear to have been used in more than the single sense, although the expression "standing crop" has been used in the sense here given to "stock."

In the following sections the data already presented will be used to develop estimates of these three quantities as well as of the quantity of food used in the production and maintenance of the trout, and the relation between this and the lower levels of the chain from which it is derived will be considered.

2. THE STOCK

This quantity is considered first since it is relatively simple to measure, and it also provides a basis for the estimation of some of the other quantities to be considered. The stock at any given time is the total weight of all the living individuals of the species or group concerned within the ecosystem at that time. This may often be most conveniently estimated as the sum of the products of number of individuals and mean individual weight for all the homogeneous groups within the population. In the present instance suitable groups are formed by the members of each year-class in each of the zones into which the stream was divided. Estimates of the numbers in these groups on several dates have already been set out, and we have seen that the mean individual weight within each group at any time can also be determined with considerable accuracy.

The estimated weight of each year-class in each zone at the time of each routine netting is set out in Table 58. These weights have been calculated from the numbers of each class shown in Table 30, and from the mean weights, interpolated where necessary, shown in Tables 38 to 41. The density by weight of the total population in each zone on each date has been calculated by using the areas of the zones given in Table 6. Although the population weights are given in kg. the densities have been converted into lb. per acre in order to facilitate comparisons, since the great majority of the published estimates of the density of trout populations in streams appear to be in these units. The total weight of the trout population of the Horokiwi remained practically constant during the period covered by the first four observations, since the differences between the estimates are negligible when compared to the probable errors. A very pronounced decrease occurred in the weight of the trout stock between May, 1941 and October, 1941, and this caused the weight of the stock in October, 1941 to be very much below that for October, 1940. This decrease was the combined result of the abnormal reduction in numbers of trout between May and October, 1941 and the relatively slow growth rate in this period. The decrease in numbers was, however, probably the more important of these two factors. The estimates of the stock in each zone also remain unexpectedly constant for the first four observation dates. In each zone the range of variation of the four readings about the mean is of the order of $\pm$ 20 per cent., which is less than would be expected from the 95 per cent. confidence limits of $\pm$ 50 per cent. which have been shown to apply to these estimates. When the

TABLE 58. The estimated total weight in kg. of each year-class in each zone at the time of each routine netting, and the estimated density (D) in lb./acre of the total trout population.

DATE.	YEAR-CLASS.	ZONE I. Wt.	I. D.	II M. Wt.	II M. D.	II R. Wt.	II R. D.	III. Wt.	III. D.	IV. Wt.	IV. D.	V. Wt.	V. D.	Total. Wt.	Total. D.
July, 1940 ..	1939	79		160		36		48		24		12		360	
	1938	133		64		13		96		36		3		345	
	1937	84		33		10		0		82		4		212	
	1936	9		0		6		58		14		4		91	
	1935	22		5		0		0		2		0		29	
	1934	22		5		0		0		2		0		29	
	Total	348	215	267	281	67	104	202	222	159	366	23	168	1,066	228
October, 1940 ..	1940	23		11		3		18		16		1		72	
	1939	136		192		42		53		73		22		519	
	1938	161		75		15		126		46		4		427	
	1937	47		19		5		0		40		2		113	
	1936	2		0		1		11		2		1		17	
	1935	18		4		0		0		1		0		23	
	1934	18		4		0		0		1		0		23	
	Total	405	250	305	322	67	104	207	229	180	414	30	220	1,194	255
January, 1941..	1940	86		29		6		17		7		1		146	
	1939	301		207		45		70		59		21		702	
	1938	46		21		4		37		14		2		123	
	1937	45		16		5		0		33		2		103	
	1936	2		0		1		9		2		0		15	
	1935	6		2		0		0		0		0		9	
	1934	6		2		0		0		0		0		9	
	Total	492	304	277	292	62	98	133	146	116	266	27	195	1,107	236
May, 1941 ..	1940	151		159		36		28		6		7		387	
	1939	118		179		42		115		67		20		543	
	1938	25		12		2		21		8		1		68	
	1937	26		11		3		0		17		1		59	
	1936	2		0		1		8		1		0		13	
	1935	3		1		0		0		0		0		4	
	1934	3		1		0		0		0		0		4	
	Total	328	203	363	382	85	133	172	190	100	232	30	218	1,078	230
October, 1941 ..	1940	14		60		1		13		41		1		130	
	1939	0		49		11		0		28		22		110	
	1938	11		6		2		9		3		0		32	
	Total	25	16	115	122	14	22	21	24	73	167	23	165	271	58
Mean total, July 1940 – May 1941		393	243	303	319	70	110	179	197	139	319	27	201	1,111	237

significance of the differences between the mean values for the various zones is considered in the light of these results, the following conclusions may be reached: the population density of Zone II R is probably significantly less than that of any other zone; there is no significant difference between the population densities of Zones II M and IV, or between Zones III and V; the differences between these two pairs of zones, or between either of them and Zone I, are of doubtful significance. In the Main Water the population density of Zone II M is probably higher than that of Zone I, while in the Road Branch the descending order of densities is probably: Zone IV, Zones III and V together, Zone II R.

The data also make it possible to follow the changes in the mass of a year-class during its life. While only one year's observations on any single year-class are available, a composite picture may be built up from the data obtained for the several year-classes which were present during the period studied, and this is shown graphically in Figs. 15 and 16. In order to reduce the irregularities as much as possible the results have been grouped in the same way as the data on angling catches, i.e., Zones I and II together as the lower waters, and Zones III, IV and V together as the upper waters. When the results of a single zone are examined, it is evident that there are major variations in the relative strength of the year-classes, particularly in the Road Branch, and that these apparently differ in different zones. The most striking of these variations are the weakness of the 1937 year-class, and relatively great strength of the 1936 year-class, in Zone III; in Zone IV the relative strength of these two year-classes appears to be reversed, although the difference is not as great.

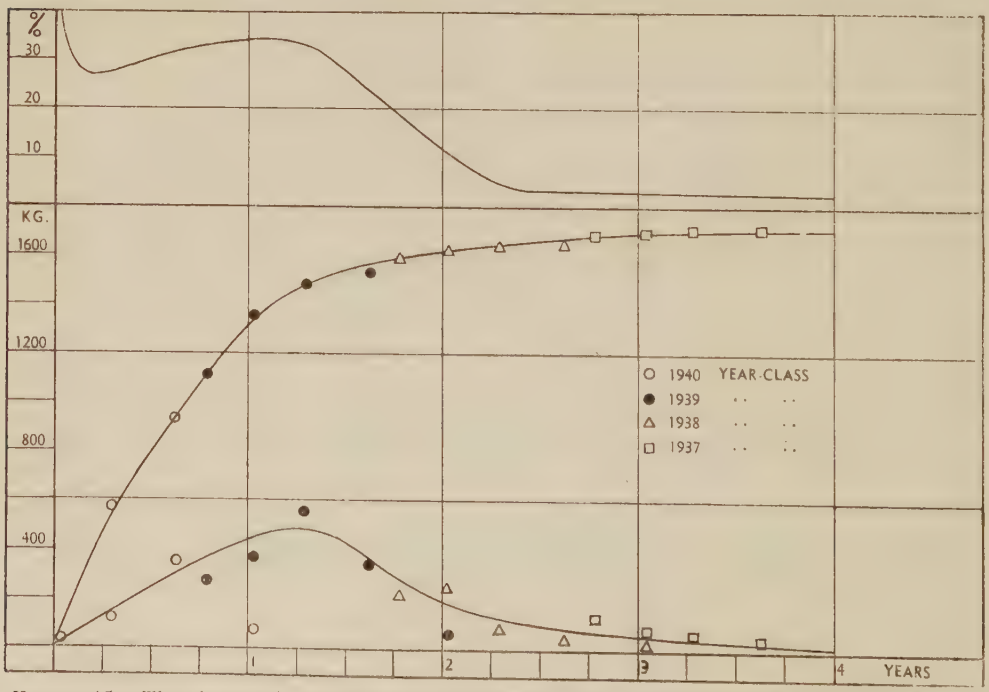

FIGURE 15. The changes in the weight of the stock and in the accumulated production during the life of a composite year-class in the lower waters. Also the changes in the stock expressed as a percentage of the accumulated production up to the same time.

The changes in the mass of a normal year-class during its life are essentially similar in all zones, although certain differences between the upper and lower waters are apparent. During the first year and the first part of the second the mass increases, as the rate of increase in weight of the individuals exceeds the rate at which they are being removed by death. This relationship is reversed during the second year, and the mass of the year-class decreases as growth is overtaken by deaths. The initial rate of increase is very much faster in the lower waters than in the upper waters, probably as a result of the greater growth rate in the lower parts of the stream. The weight of the year-class is at its maximum at about the middle of the second summer in the lower waters and it then decreases sharply. In the upper waters the mass seems to continue to increase during the second summer, and does not begin to decline until the following spring. It is noticeable that the mass of the year-class begins to decrease at about the time of the change-over between the two sections of the growth curve. The earlier and more rapid decrease in the lower waters may be due to the earlier and more intensive cropping by anglers in these waters. In all parts of the Horokiwi the peak of the mass curve occurs much earlier than in the brown trout of Crystal Creek in New York, where Schuck (1945) found the peak occurring in the fourth year. The growth rate was very much slower in that stream than in the Horokiwi, and it is of interest, and possibly significant, that the mean length of the fish when the weight of the stock was at a maximum was about 26 cm., which is very close to the length of the Horokiwi fish at their peak. The mortality rate in Crystal Creek has already been mentioned as being slightly less than in the Horokiwi, and

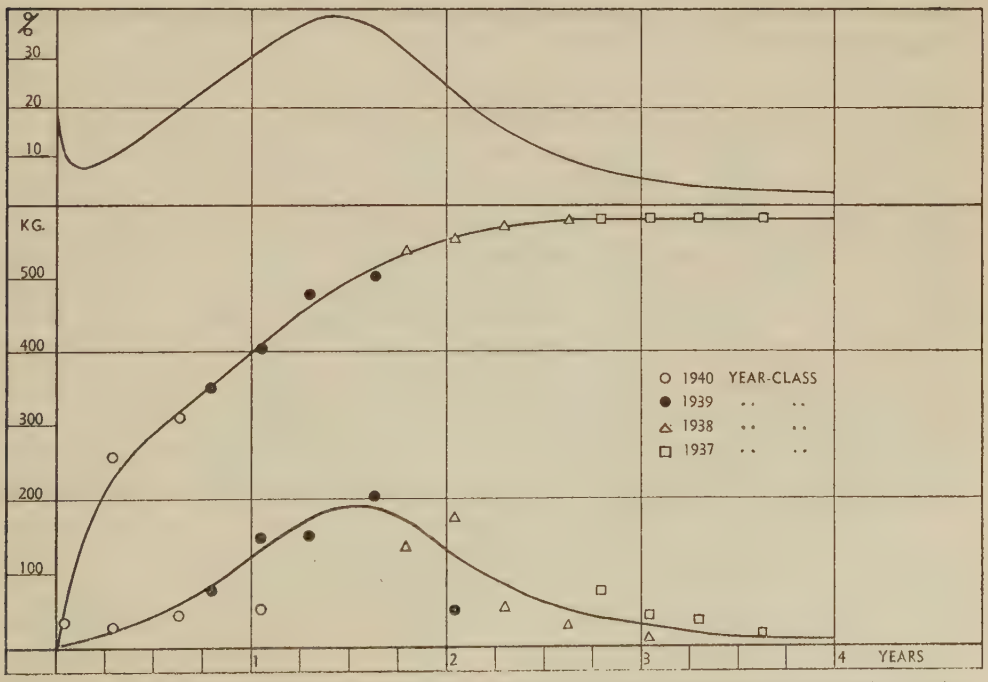

FIGURE 16. The changes in the weight of the stock and in the accumulated production during the life of a composite year-class in the upper waters. Also the changes in the stock expressed as a percentage of the accumulated production up to the same time.

angling was only responsible for about 15 per cent. of the deaths of legal-sized fish.

The estimated density of the trout stock of the Horokiwi may be compared with some of the data which are available for fish stocks in other waters. In New Hampshire, Hoover and Merrill (quoted by Needham, 1940) found the average density of the trout stock in two small streams to be 35.7 lb./acre, while other species of fish present brought the total density up to 41.4 lb./acre. In Michigan, studies of a number of trout streams have shown trout stocks ranging between 1.4 and 96.9 lb./acre, with total stocks between 4.1 and 178.0 lb./acre (Shetter and Hazzard, 1939, and Shetter and Leonard, 1943). In New York, Schuck (*loc. sit.*) found the mean density of the trout stock of Crystal Creek to be 13.8 lb./acre; other species of fish do not appear to have been present.

Higher densities are recorded by Needham, Moffett and Slater (1945) from Convict Creek in California, which contains only trout. The density of the stock appeared to be significantly affected by angling in this instance, since the density in a section closed to angling varied in different years between 214 and 434 lb./acre, while in the same period the density in another section in which angling was permitted was between 40 and 146 lb./acre.

The density of the trout stock in the Horokiwi thus appears to be higher than has been usually recorded in North American trout streams. In addition to supporting over 200 lb. per acre of trout, the Horokiwi also contains a stock of native fish of unknown density. The work of Burnet (in press) suggests that the density of the eel stock is probably about 30–50 lb. per acre, but the density of the other native fish is probably negligible when compared to the trout and eels, except in the lower part of Zone I.

3. PRODUCTION

Of the three quantities referred to earlier in this discussion, both the stock and the crop can be measured directly by suitable methods. Production on the other hand, being a dynamic rather than a static quantity, can only be measured by indirect means, and must be computed from quantities which can be observed directly. A number of methods of doing this are possible, and have been used with varying degrees of soundness by different workers. Juday (1940) and Lindeman (1941) have expressed the annual production of plankton and bottom fauna in lakes as the product of the average stock and the number of "turn-overs"—apparently equivalent to life-cycles—of the organisms concerned in a year. This method actually gives an under-estimate of the annual production because it is based on the incorrect assumption that the stock of every generation at any moment of sampling must be equal to the total production of that generation, whereas the stock at any moment must be less than the total production, both by the amount that has been embodied in the individuals which have died prior to sampling, and by the amount which will be added by the further growth of the surviving individuals after the sampling date. These effects would only be eliminated if all individuals survived to the end of the full life-cycle, and if sampling were only carried out at the end of each successive life-cycle, at a time when all growth had been completed, but before any individuals had been removed from the population

by death, emergence, or migration. Under all other conditions the production as determined by this method must be below the true value, possibly by a very large proportion. Juday (1940) has also estimated the production of fish as the quantity removed by angling; this quantity is actually the crop, and is less than the true production by the amount of material embodied in all the fish dying from all causes other than angling.

Borutzky (1939a and b) made an estimate of the annual production of the bottom fauna of Lake Beloie, and particularly of *Chironomus plumosus,* by estimating the number of individuals of each generation which died at each stage of the life-cycle and including them in his computations. His results must therefore be regarded as the first estimates of the production in a fresh-water community which are both theoretically sound and based on satisfactory data.

An estimate of the production of the Horokiwi trout population based on the detailed growth data and on estimates of the numbers of individuals surviving to each size was included in the preliminary account of the present work (Allen, 1946).

Ricker and Foerster (1948) have made a careful study of the production of young sockeye salmon (*O. nerka*) of Cultus Lake, making use of detailed estimates of growth and mortality rates.

The methods available for the computation of production which are theoretically satisfactory may be divided into two main types. The more direct of these is the determination of production by arithmetical or graphical methods from the raw data regarding the size and number of individuals at various times. The second type of method involves the construction of mathematical models which represent the characteristics of the population concerned over longer or shorter periods, and the computation of production by the insertion of appropriate values in formulae derived from the models. One of the simplest of such models is based on the assumption that both growth and mortality curves have a simple exponential form, and appropriate formulae for the calculation of production in this case have been put forward by Ricker (1946) and Allen (1949). This model is actually a special case of the general proposition that over any period for which the instantaneous growth rate is constant, the production is the product of this rate, the length of the period, and the mean stock. The practical application of this method is complicated by the fact that the instantaneous growth rate rarely remains constant over long periods, particularly in young fish. Ricker and Foerster (1948) have overcome this difficulty by computing production over a succession of half-month periods, changing the growth rate and mortality rate as the data demanded. This method, although it yields valuable results, is however somewhat laborious. It has recently been suggested (Allen, 1950) that other mathematical models may in some cases apply with unchanged constants over relatively long periods, and therefore simplify the computation. Growth formulae of the type discussed earlier in this paper would appear to provide a suitable basis for such models.

The graphical method of estimating production has certain advantages, although its use does not seem to have been previously described. This method depends on the fact that if the number of surviving individuals is plotted against the mean

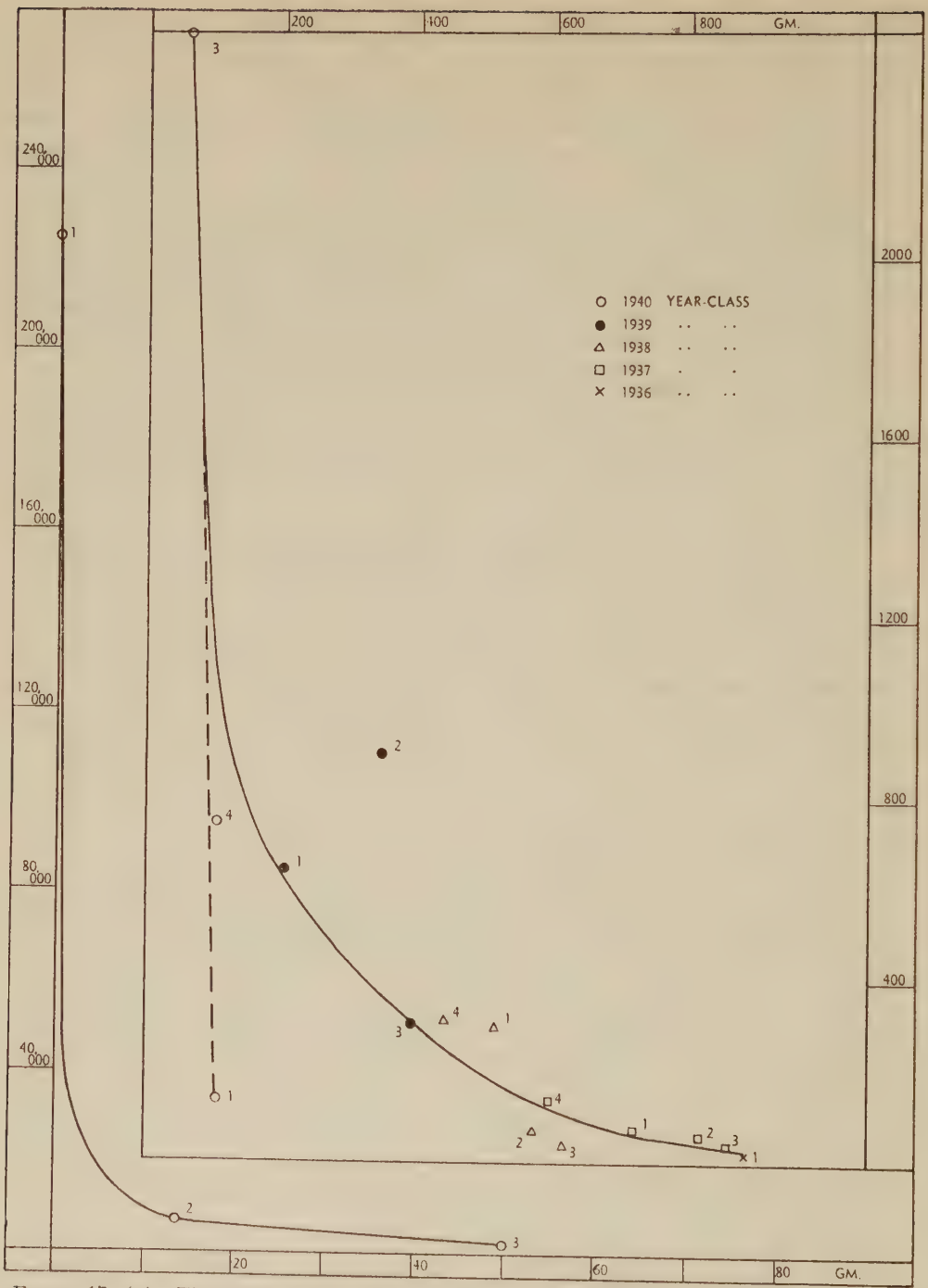

FIGURE 17. (a) The number of survivors plotted against mean individual weight at the same date for a succession of year-classes in Zone I. The figures beside the points indicate the months for which the estimates were made; 1 = October, 2 = January, 3 = May, 4 = July. The broken line leads to a point for October, 1941, when the numbers appear to have been abnormally reduced by the floods. Owing to the wide variation in numbers the early and later parts of the curve have been plotted on separate scales.

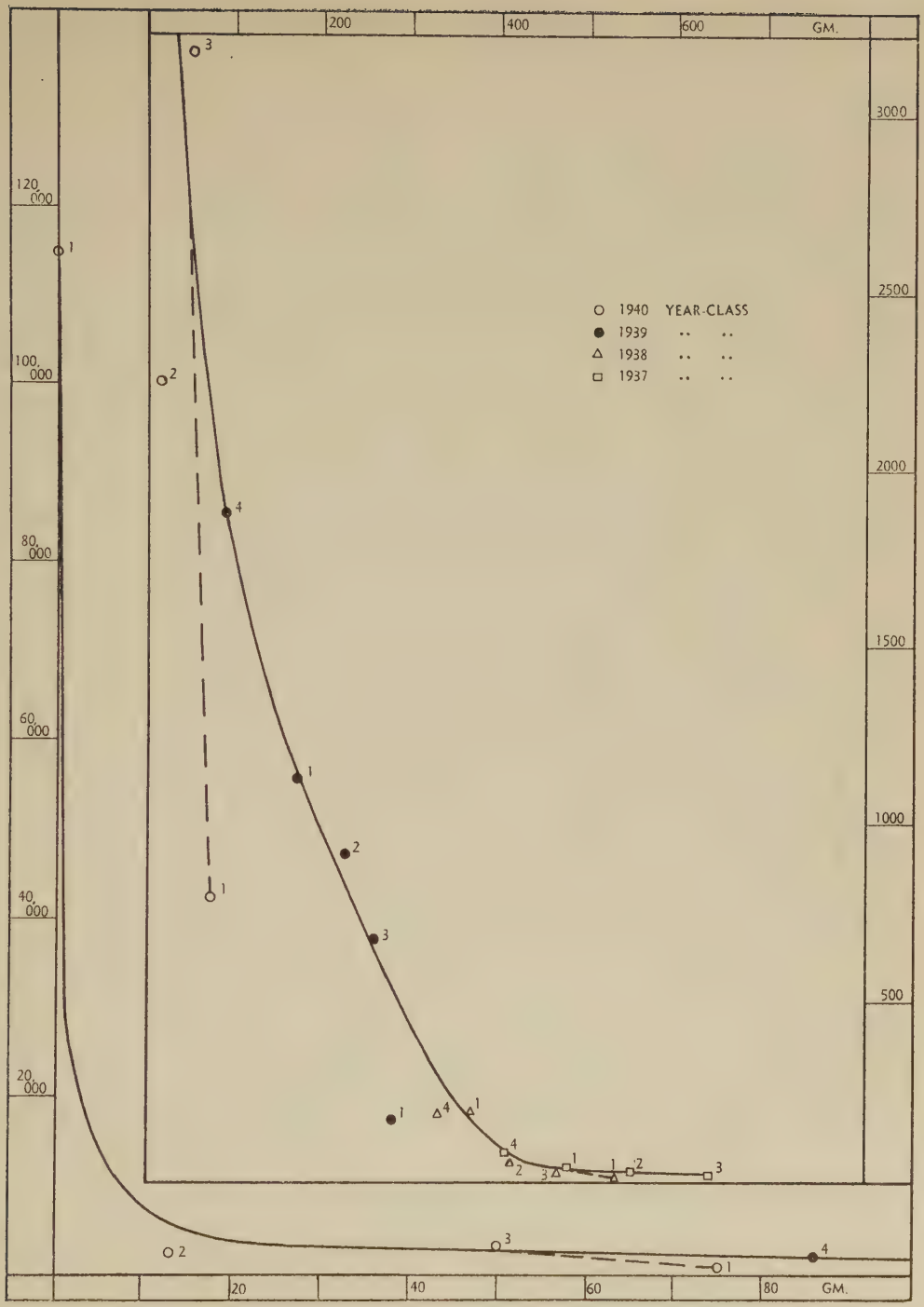

FIGURE 17. (b) The number of survivors plotted against the mean weight for Zone II M.

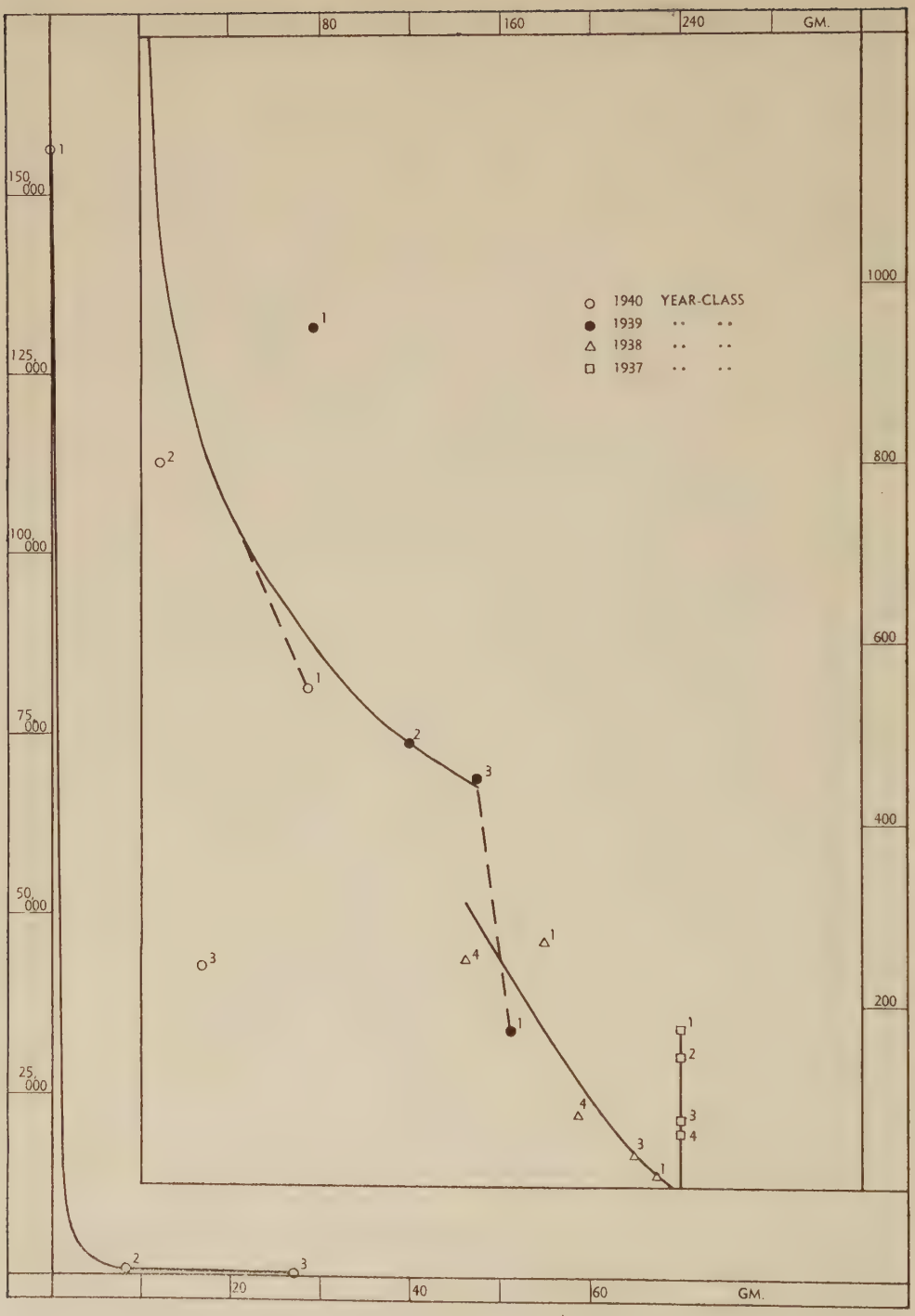

FIGURE 17. (c). The number of survivors plotted against mean weight for Zone IV.

individual weight throughout the life of a generation, the area under the curve, between any two points, equals the production in the population during the period corresponding to the selected part of the curve. Curves of this nature, based on the data for Zones I, II M, and IV, are shown in Fig. 17. This method has a twofold advantage: where the data are subject to irregular error, due to sampling and similar causes, it provides a convenient means of smoothing the results prior to computation: if the data are highly accurate it is easy to allow for the effects of real irregularities and fluctuations due to seasonal or other causes. This technique provides a clear illustration of the fallacy in the method of computing production used by Juday and Lindeman. In a diagram such as those in Fig. 17 the stock at any given time is equivalent to the area of the rectangle bounded on two sides by the axes, and having the origin and the selected point on the curve at its opposite corners. In all normal cases the number of individuals continually decreases while the mean size increases, and it is obvious that the area of any such rectangle will be less than the area under the curve up to the same point, and still less than the total area under the curve which represents the total production in the life of the generation. Therefore, the stock at any instant must obviously be less than the production up to that instant, and consequently the mean of any number of successive determinations of the stock must be less than the total production of the generation.

Attention has already been drawn to the fact that, particularly in the upper zones, there were sometimes marked differences in the relative strength of different year-classes. Allowance has been made for these differences where necessary, by drawing separate curves through the points corresponding to the abnormal year-classes in such a way that the general trends are the same as for the other year-classes at the same stage in the life-cycle. Such an effect is illustrated in Zone IV, in which the curve for the relatively weak 1938 year-class is on a lower level than that for the 1939 year-class. The 1937 year-class appears to have been numerically comparable to that of 1939, but, since the fish of the 1937 year-class had already reached their maximum size in this zone when the observations began, the year-class gave no production during the period studied and is represented by a vertical line.

Since the determinations of mean weight are a great deal more accurate than those of the number of fish in the population, the division of the areas under the curves into sections corresponding to the desired periods has been done by drawing vertical lines through the mean weights occurring at the beginning and end of each period.

Table 59 shows the production estimated by this method to have taken place in each zone during successive periods. These estimates have been made for the periods between successive routine nettings, but an estimate has also been made by extrapolation backward for the period May to July, 1940, in order to provide data for a complete year which was unaffected by floods. Although the flood of February, 1941 did have harmful effects on the trout population, these effects were not as severe, particularly on the numbers of fish, as those of the floods from July onwards in the same year. The year May, 1940 to May, 1941 consequently provides a good indication of the amount of production in a normal year, while

TABLE 59. The amount produced by the trout population (P) in kg. for successive periods in each zone and by each year-class; also the intensity of production (D) in each zone in each period in lb./acre. The total production in the period May 1940 to May 1941 is shown as representing a normal year, and the ratios between the amounts produced between May and October in 1941 and 1940.

PERIOD.	YEAR-CLASS	ZONE. I. P.	I. D.	II M. P.	II M. D.	II R. P.	II R. D.	III. P.	III. D.	IV. P.	IV. D.	V. P.	V. D.	Total. P.	Total. D.
May–July, 1940	1939	71		87		18		22		10		6		214	
	1938	16		35		6		25		8		2		92	
	1937	10		24		4		0		0		0		38	
	Total	97	60	146	154	28	43	47	52	18	41	8	60	344	73
July–Oct., 1940	1939	85		125		29		20		25		8		292	
	1938	18		9		2		8		8		1		46	
	1937	12		3		1		0		0		0		16	
	Total	115	71	137	144	32	49	28	31	33	76	9	65	354	75
Oct., 1940,— Jan., 1941	1940	328		211		49		144		107		7		846	
	1939	67		56		11		47		23		6		210	
	1938	8		5		1		8		2		1		25	
	1937	5		2		1		0		0		0		8	
	Total	408	251	274	287	62	96	199	219	132	304	14	98	1,089	232
Jan.–May, 1941	1940	186		125		30		31		17		6		395	
	1939	22		24		5		0		14		10		75	
	1938	3		3		1		8		2		0		17	
	1937	2		2		0		0		0		0		4	
	Total	213	131	154	162	36	56	39	43	33	76	16	118	491	105
May–Oct., 1941	1940	53		39		10		17		33		5		157	
	1939	1		9		1		0		5		0		15	
	1938	0		1		0		1		0		0		3	
	1937	1		0		0		0		0		0		1	
	Total	55	34	49	52	11	18	18	19	38	87	5	35	176	37
May, 1940, to May, 1941	Total	833	512	711	747	158	245	313	344	216	497	47	342	2,278	485
May–Oct., 1941: May–Oct., 1940		0·26		0·17		0·19		0·23		0·74		0·27		0·25	

comparison between the periods May–October, 1941 and May–October, 1940, which is also made in the table, gives a measure of the extent to which the heavy winter floods of 1941 reduced the production of trout.

The differences in the intensity of production in the various zones closely follow those of the density of stock shown in Table 58. This is only to be expected, since the rate of production is the product of the stock and the instantaneous growth rate, and it has already been shown that the differences in growth rate between the various zones at any one time are small compared to the differences between successive stages in the life-cycle. The differences in growth rate between the zones are however sufficiently large to cause the production to be greater in relation to stock in the lower waters than in the upper waters.

Production was at a very much lower level during the winter of 1941 than in the previous year. It is apparent from the data already discussed that this was due partly to the unusually low growth rate in that year, and particularly to the great reduction in the number of trout in 1941. We have already seen that these effects were largely the result of the severe winter floods of that year, and the reduced production may therefore be ascribed to the same cause. Zone II, which was found to have suffered most severely from the floods in all the aspects previously considered, also showed the greatest reduction in the production rate, which was about one-sixth of that of the preceding, more normal, winter.

By combining the data for the various year-classes, it is possible to examine the way in which the production within a single typical year-class is distributed through its life. In order to reduce irregularities due to variations in the relative strengths of different year-classes, the zones have been grouped into the lower and upper waters. Table 60 shows the accumulated production of the composite year-class in each part of the stream at a succession of dates. The results are also presented graphically in Figs. 15 and 16 where they may be compared with the changes in the stock of the same composite year-class. It is evident that most of the production takes place in about the first year and a half of the life of each year-class. In the lower waters the rate of production slows down very abruptly at about the middle of the second summer; in the upper waters the slowing down is more gradual, and seems to be spread over much of the second year. In both parts of the stream, however, production is concentrated almost entirely in the first two years, the percentage of the estimated total production of the year-class which has been achieved by the end of the second year being 94.9 per cent. and 96.3 per cent. in the lower and upper waters respectively.

TABLE 60. The estimated accumulated production in kg. at the end of successive periods in the life of a composite year-class in the lower and upper waters. Data drawn from the production of the various year-classes shown in the previous table.

YEAR-CLASS	LOWER WATERS. 1940.	1939.	1938.	1937.	UPPER WATERS. 1940.	1939.	1938.	1937.
October–January	588	..	..	..	258	..	..	..
January–May	929	..	..	..	312	..	..	..
May–July	..	1,105	1,586	1,674	..	350	538	576
July–October	..	1,344	1,615	1,690	..	403	555	576
October–January	..	1,478	1,629	1,698	..	479	566	576
January–May	..	1,529	1,636	1,702	..	503	576	576

It is clear from the figures that there is generally good agreement between the points, and that, particularly in the lower waters, they lie closely along a smooth curve. The basic quantities involved in the estimation of production are the mean weight and the number of fish in the population. The probable errors in the determination of mean weight have been shown to be very small compared to those in the determination of number, and consequently the accuracy of the estimates of production, like those of stock, is essentially the same as that of the numbers in the population. The probable limits of the estimates of numbers have been shown to be, at the best, about ± 50 per cent. for any single estimate, although there is some increase in the reliability when a number of estimates in good agreement are considered together, and this range will also apply to the estimates of production.

When the distribution during the life of a year-class of quantities such as stock or production, which depend on the population estimates, is considered, the shape of the curves, as distinct from their absolute height, depends only on the relationship between successive observations. In the discussion of the errors in the estimation of population, it was shown that one of the major sources of error lay in the estimate of netting efficiency. This factor was applied equally to all estimates, and therefore does not affect the shape of the curves. If this is ignored, the probable limits of the sampling errors are reduced to about ± 25 per cent. for the most numerous 1940 and 1939 year-classes. In view of this, and of the generally good degree of agreement between successive points, the shape of the stock and production curves, and the relation between them, can be accepted as being reasonably reliable. The most doubtful section of the production curves is that between October and January of the first year. The mortality rate is apparently changing rapidly at this time, and the lack of intermediate population observations makes it impossible to examine directly the nature of the change. The production estimates given in the table are based on free-hand curves which follow approximately the line corresponding to a constant instantaneous growth rate during this period. It seems not unlikely that the mortality rate is in fact relatively high at the beginning of this period and then decreases fairly rapidly; the estimates would therefore tend to be on the high side of the actual figures. On the other hand, if, as seems possible, the population in January of the first year has been under-estimated, the stock and production up to this time will also tend to be under-estimated. Thus the two major possible errors which may particularly affect the estimates of production during the first three months will act in opposite directions and may tend to cancel each other.

Throughout the life of a year-class the process of production, or the incorporation of additional matter into the trout, is going on continuously although at a decreasing rate. The amount of matter which is actually embodied in the year-class to form the stock at any instant increases for a time, but subsequently falls gradually to zero as production is outstripped by removals by death. The stock at any time is thus the difference between the production up to that time and the removals by death; the stock is in fact the surviving portion of the production.

From the smoothed curves fitted to the points in Figs. 15 and 16 the proportion of the production which is surviving, i.e., the stock : production ratio, has been calculated and is plotted in the upper section of each figure. The general trend of

the curves is similar in both sections of the stream. Stock and production are at first identical, since both are represented by the weight of fry which begins the new generation. The high mortality rate in the early months very rapidly reduces the proportion of the accumulated production which survives, although the stock is increasing slowly at this time. As the mortality rate soon decreases, while the growth rate remains high, the surviving proportion of the production ceases to fall and actually begins to rise slowly before levelling off at a fairly flat maximum at about the beginning of the second year. During the second year the rate of growth decreases while the mortality rate increases slightly, and consequently the stock begins to decline. Since production is still continuing at this time the proportion which is surviving as the stock falls slightly sooner and more rapidly than does the stock itself. Thus, in the Horokiwi the proportion of the production which survives as the stock is never higher than about 30–35 per cent., and by the end of the second year has fallen to about 12 per cent. in the lower waters and 20 per cent. in the upper waters. If, as has been suggested, the production of the first few months has been over-estimated, then the actual surviving percentages will be somewhat higher, but the essential shape of the survival curve will be unchanged and the surviving proportion of the production will still fall off rapidly after about the middle of the second year.

4. THE CROP

It has now become possible to consider the angling catches recorded in a previous section in relation to the estimates of stock and production, and to examine the way in which the crop is related to the production from which it is derived. The population and the crop are compared numerically in Table 61. This comparison is based on the 1940–41 angling season, since this is the only one of those studied which lies within the period covered by the estimates of stock and production. Although the war had been in progress for over a year when this season began, we have already seen that the intensity of the angling effort had so far been little affected, and was only about 15 per cent. below that of 1939–40, which was probably an almost normal season. The trout population and angling conditions were both adversely affected to some extent in the last few months of the season by the flood of 13th February, 1941. Most of the season, including the early part which usually provides most of the angling in the Horokiwi, was however perfectly normal. The relation between the angling catch and the trout population in the 1940–41 season may therefore be regarded as typical of the conditions which existed for at least the few years prior to this date.

In the table the decrease in the estimated population of each year-class between the nettings of October, 1940 and April–June, 1941 is compared with the number of fish believed to have been removed by angling. The October netting was carried out between 25th October and 1st November in the lower waters, and between 11th and 18th October in the upper waters; the April–June nettings were made between 22nd April and 26th May in the lower waters and 29th May and 15th June in the upper waters. The angling season extended from 1st October, 1940 to 30th April, 1941 inclusive; the period covered by the netting therefore both began and ended slightly later than the angling season, and the

TABLE 61. Comparison for each year-class between the decrease in the population and the removals by angling in the 1940–41 season; results shown separately for the lower and upper waters.

YEAR-CLASS.	LOWER WATERS. 1940.	1939.	1938.	1937.	1936 and earlier.	1938 and earlier.	UPPER WATERS. 1940.	1939.	1938.	1937.	1936 and earlier.	1937 and earlier.
Population at October, 1940	367,000	2,030	550	115	56	721	345,000	1,670	735	180	48	228
Population at May, 1941	6,420	1,140	70	52	14	136	780	1,160	97	78	28	106
Decrease	361,000	890	480	63	42	585	344,000	510	638	102	20	122
Angling catch, 1940–41..	..	81	153	36	5	194	..	..	2	9	4	13
Percentage angling catch in decrease	0	9·1	31·8	57·3	11·9	33·1	0	0	0·3	8·8	25·0	10·7

difference was most pronounced at the end of the season in the upper waters. In view of the rather wide limits of accuracy of the population estimates, the coincidence between the two periods seems sufficiently close to enable satisfactory comparisons to be made. The data for the year-classes prior to 1937 have been grouped together in the table on account both of the relatively large probable errors of the small numbers involved in these population estimates, and of the practical impossibility of distinguishing between these older year-classes in the angling catches.

In the lower waters fish only begin to reach the legal size limit, 11 inches (27.9 cm.), during their second summer, and consequently none of the decrease in the 1940 year-class, and only a small proportion of that in the 1939 year-class was due to angling; in the older year-classes, however, angling is a relatively important cause of mortality. Since all the older year-classes are fully available to anglers the results for all year-classes older than 1939 have been combined in the last column of the "lower waters" section of the table in order to reduce the random variations as much as possible. It appears that in these age-groups angling is responsible for about one-third of the mortality which takes place during the angling season; there is however further mortality in the close season due to natural causes. The proportion of the total mortality which is caused by angling is thus less than one-third even in the age-groups which are legally fully vulnerable to anglers.

The lower growth rate of the trout in the upper waters has important effects on the relation between the angling catch and the population. The fish are generally at least a year older before they reach the legal limit, and consequently no fish of the 1940 and 1939 year-classes, and only a very few of the 1938 year-class, figured in the angling catch of 1940–41. In this section of the table the results for all year-classes older than 1938 have been grouped together in the right-hand column. It is evident that the proportion of the mortality in the takeable year-classes during the season which can be ascribed to angling is much less in this part of the stream than in the lower waters, being only about 10 per cent. This difference is probably due mainly to the much lower intensity of angling in the upper waters; in 1940–41 an average of 105 hours of angling was recorded for each mile of the lower waters, as against 6 hours per mile on the upper waters. In the 1941–42 and 1943–44 seasons the angling intensity on the upper waters was as high as 25 and 37 hours per mile respectively, and it appears that, if the total mortality

was similar to that in 1940–41, the proportion due to angling was about one-third, and so was similar to that in the lower waters under normal conditions.

TABLE 62. Comparison for each year-class between the stock initially present, the amount produced and the part removed as the angling crop, all in kg., in the 1940-41 season; results shown separately for the upper and lower waters.

YEAR-CLASS.	LOWER WATERS.						UPPER WATERS.					
	1940.	1939.	1938.	1937.	1936 and earlier.	1938 and earlier.	1940.	1939.	1938.	1937.	1936 and earlier.	1937 and earlier.
Stock at October, 1940	37	371	251	71	47	369	35	148	176	42	17	59
Production, October–May	588	186	21	13	0	34	258	101	20	0	0	0
Total	625	557	272	84	47	403	293	249	196	42	17	59
Stock at May, 1941 ..	346	339	39	40	11	90	41	203	29	19	9	28
Loss, October–May ..	279	218	233	44	36	313	252	46	167	23	8	31
Angling crop, 1940–41	0	21	66	20	4	90	0	0	0·5	3	2	5
Percentage angling crop in loss	0	9·6	28·6	45·5	11·1	28·7	0	0	0·3	13·0	25·0	16·1

The crop may also be compared with the stock and production on a weight basis. This problem is however more complex, since the comparison is being made not with the number of fish present, which is subject only to a continuous decrease, but with the weight of the stock, which is the balance between the ever-increasing production due to growth and the removals due to mortality. Table 62 summarizes this aspect of the events of the 1940-41 season. The total amount lost to any year-class during a season is the sum of the stock at the beginning and the production during the season, less the stock at the end of the season. It appears that in 1940–41, in the lower waters, angling caused about 10 per cent. of the seasonal loss in the 1939 year-class, and about one-third of the loss in the older year-classes. In the upper waters angling made little or no contribution to the loss in the first three year-classes, but caused about one-sixth of the loss in the older fish.

The above discussion has been limited to events within a single angling season, but a more instructive picture of the relationship between crop and production in a trout population can be obtained by following events through the life of a single generation. Although no single year-class was followed throughout its life, a composite year-class may be built up by combining the results obtained from the various year-classes between October, 1940 and May, 1941. This has been done in Table 63; the accumulated production of the composite year-class has been taken from Table 60, and the stock from Table 58. The accumulated loss at any date is the amount of material which has been withdrawn permanently from the year-class up to that time by deaths and, possibly, by emigration, and is the difference between the accumulated production and the stock. The accumulated crop is the sum of all the angling catches taken from the year-class up to the given date. It is evident that a great part of the ultimate total production has already been lost before cropping begins. In the lower waters cropping normally begins early in the second summer, and in the upper waters early in the third summer, although in both cases the angling catch in the first cropping season is relatively light. In the lower waters we see that 973 kg. out of an ultimate total

TABLE 63. The relation between the accumulated crop, production and loss, all in kg., in a composite year-class in the lower and upper waters.

Year-class.	Lower Waters. 1940. Oct.	May.	1939. Oct.	May.	1938. Oct.	May.	1937. Oct.	May.	1936. Oct.	May.	Upper Waters. 1940. Oct.	May.	1939. Oct.	May.	1938. Oct.	May.	1937. Oct.	May.	1936. Oct.	May.
Accumulated production	37	929	1,344	1,529	1,615	1,636	1,690	1,702	1,702	1,702	35	312	403	503	555	576	576	576	576	576
Stock	37	346	371	339	251	39	71	40	3	3	35	41	148	203	176	29	42	19	14	9
Loss	0	583	973	1,190	1,364	1,597	1,619	1,662	1,699	1,699	0	271	255	300	379	547	534	557	562	567
Accumulated crop ..	0	0	0	21	21	87	87	107	107	111	0	0	0	0	0	0·5	0·5	3·5	3·5	5
Percentage crop in loss	0	0	0	1·8	1·5	5·5	5·4	6·4	6·3	6·5	0	0	0	0	0	0·1	0·1	0·6	0·6	0·9

production of 1,702 kg., or 57.1 per cent., has been lost before cropping begins; in the upper waters the corresponding figures are 379 kg. out of 576 kg., or 65.8 per cent. During the first cropping season and the following close season natural mortality continues at a high rate, and the second cropping season, which is the first in which all the fish are legally takeable, is entered with losses already amounting to 1,364 kg. in the lower waters, and to 534 kg. in the upper waters. These amounts form respectively 80.3 per cent. and 92.7 per cent. of the ultimate total production, and the crop has only contributed 21 kg. and 0.5 kg., or 1.5 per cent. and 0.1 per cent. towards them. In the remaining years cropping is more efficient, and accounts for 90 kg. out of the last 335 kg. of loss in the lower waters, and 4.5 kg. out of the last 33 kg. in the upper waters.

The relation between production, stock and crop is shown graphically in Figs. 18 and 19. The smooth curves for production and stock have been taken from Figs. 15 and 16, stock being measured downwards from the production curve instead of upwards from the horizontal axis. The points, taken from Table 63, on which the accumulated crop curve was based, were, in turn, plotted downwards from the stock curve. The distance between the crop curve and the horizontal azis therefore represents the amount of the production up to any time which has been lost by non-angling deaths, or, possibly, by migration. The diagrams show very clearly that a large proportion of the ultimate total production has already been lost before angling commences, and that, even in the lower waters, the crop forms only a small proportion of the part of the production which is still available.

We have already seen that the difference in the proportion of the takeable fish which is caught by anglers in the upper and lower waters is correlated with the relative intensity of angling, and this factor should also be taken into account in comparing the Horokiwi results with data from other waters. Comparable data are provided by the work of Schuck (1945) on Crystal Creek, a stream of about the same size as the lower waters of the Horokiwi. Here an angling intensity of 80 to 130 hours per mile caused about 15 per cent. of the total annual mortality among takeable fish. The total annual mortality was similar to that in the Horokiwi, and since about 30 per cent. of the mortality in the seven-months season in the Horokiwi is due to angling it appears that similar angling pressure is making similar contributions to the total mortality in these two streams. In the Michigan waters studied by Shetter and Leonard (1943) about half of the total annual loss of 86 per cent. was caused by angling, but no data regarding the intensity of angling are available. In Convict Creek, California, where the decrease in the population during the angling season was between 43 per cent. and 52 per cent., Needham, Moffett and Slater (1945) considered, without producing evidence, that "the anglers' take was probably close to the observed losses."

The angling yield may also be expressed as a proportion of the takeable fish present at the beginning of the season. In the Horokiwi this was 194 out of 721, or 27 per cent., in the lower waters, and 13 out of 228, or 6 per cent., in the upper waters. More data are available for comparison when the results are expressed in this form. In Crystal Creek Schuck (1945) found that in the three seasons studied the proportion of the initial population removed by angling ranged

between 15 per cent. and 28 per cent., and, as we have seen, the angling intensity was similar to that in the Horokiwi. In an earlier experiment the same worker (Schuck, 1942) found that in three separate weeks, in each of which the intensity of angling was about 190 hours per mile, the proportion of the initial population

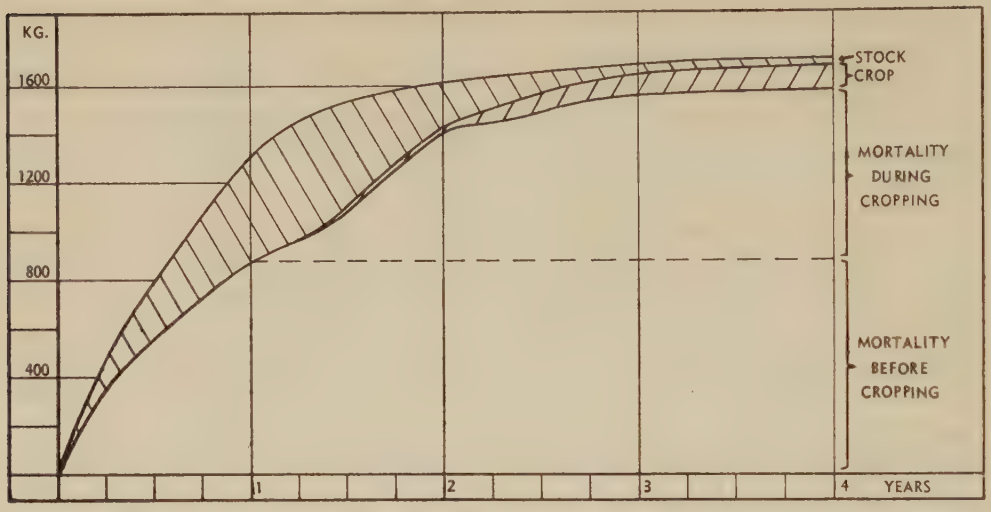

FIGURE 18. The development of the accumulated production during the first four years of the life of a normal year-class in the lower waters; showing the amount which survives as the stock, the amount which has been removed as the angling crop, and the amount dying from other causes.

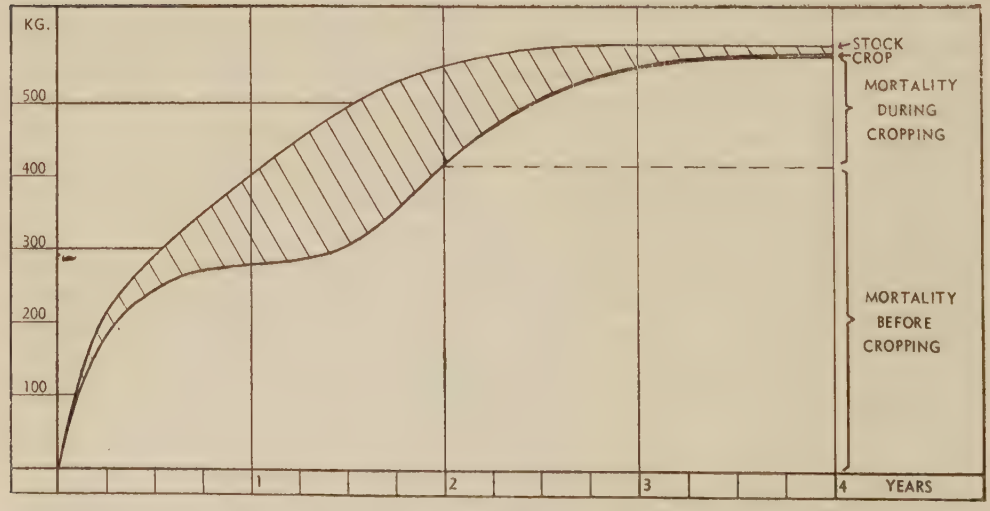

FIGURE 19. The development of the accumulated production during the first four years of the life of a normal year-class in the upper waters; showing the amount which survives as the stock, the amount which has been removed as the angling crop, and the amount dying from other causes.

which was taken ranged between 12 per cent. and 25 per cent. Thus, the same proportion of the stock as before was removed by a similar angling intensity, although in this case the effect of simultaneous natural mortalities would be less on account of the short duration of the observations. A number of similar observations by other workers are reviewed by Hobbs (1948), who found that the average proportion of the initial population taken by anglers in one year was 37.5 per cent. for all species of trout, but was only 13.8 per cent. for brown trout. Very much higher proportions, ranging between 65 per cent. and 92 per cent., were recorded by Thorpe, Rayner and Webster (1947), but in this case the intensity of angling was high, being 5,740 hours per mile for the season.

5. PRODUCTION AND FOOD SUPPLY

In the preceding sections the production, stock and crop of the Horokiwi trout population have been estimated. From these data, and from the results of various studies of the food requirements of fish under experimental conditions, the approximate food consumption of the population can be determined and compared with the amounts available. The food requirements of salmonid fishes have been studied by Brown (1946), Pentelow (1939) and Surber (1935). While Brown's work was detailed and carefully controlled, the results are not closely applicable to the present problem, partly because the food used, raw beef, was of very different composition to that taken by trout under natural conditions, but mainly because the food intake was measured not as food ingested but as food assimilated. The work of Karzinkin (1939) indicates that the difference between these two quantities is variable and may be as high as 30 per cent. Surber fed trout on natural food (*Gammarus fasciatus*), and measured the actual food intake, but his observations are limited in extent. The most valuable results for present purposes are therefore those of Pentelow, who conducted a long series of experiments, in which the growth of brown trout fed on known amounts of *Gammarus pulex* was measured. Although Pentelow's results indicate that the food-growth relationship is affected by temperature, and, in particular, that the efficiency of conversion falls with increasing temperature, there are not sufficient data to enable these effects to be allowed for in computing the food consumption in the Horokiwi. Pentelow's observations were however made in approximately the same range of temperatures as occurs in the Horokiwi, and the application of his mean results should therefore give a reasonably correct estimate of the total food consumption, although it may lead to minor irregularities in the relative amounts consumed at different seasons. The growth rates set out in Pentelow's Table IV are expressed as a proportion of the weight at the beginning of the observed period, and the actual value consequently depends to some extent on the length of the observed period, which was variable. It was therefore considered better to transform these growth rates into instantaneous rates on a daily basis, i.e., k in the formula on page 121. The food consumption in Pentelow's data was expressed as a proportion of the mean body weight for the period and appears to be sufficiently close to the true instantaneous rate to require only transformation from a weekly to a daily basis. The results given in Pentelow's Table IV are plotted in Fig. 20 after being transformed in this way, and grouped, and it appears that a fairly linear relation

exists. A regression line has been fitted to these points by the method of least squares, giving the result:—

$$f = 0.0123 + 4.205\ k$$

where f is the food intake in proportion of body weight per day, and k is as before. The maintenance ration required to maintain a fish at constant weight is therefore 1.23 per cent. per day; and the efficiency of conversion of food in excess of the maintenance ration is given by

$$\frac{1}{4.205} = 0.238$$

Fig. 20 shows also Brown's data for brown trout at 11.5° C, re-calculated on a daily basis from her Table 2 in Part II, as well as Surber's data for both rainbow (*S. gairdnerii*) and brook trout (*S. fontinalis*). Both these results are clearly in fairly good agreement with those of Pentelow. The downward trend at the upper

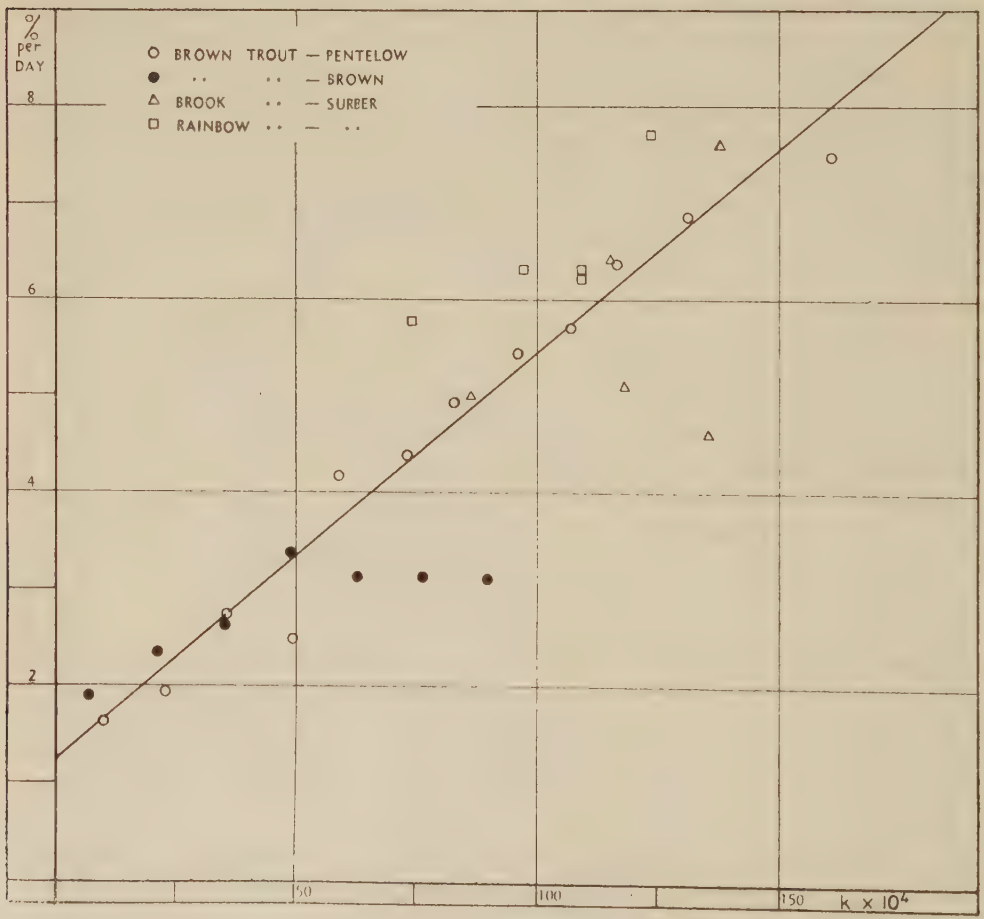

FIGURE 20. The relation between the food consumption of trout (in % per day) and the instantaneous growth-rate (k). Data taken from the three workers quoted, the solid line is the regression line fitted to Pentelow's data.

end of Brown's data may be due to the fact that they apply to assimilated and not ingested food.

These two constants, the maintenance requirement and the efficiency of conversion, can be used to estimate the food requirements of the Horokiwi trout population. Some errors may arise through applying these figures to trout of all ages at all seasons. Brown (1946) has shown that the maintenance requirement of trout, as determined for assimilated food, decreases with increasing size, and is equal to 1.23 per cent. per day for trout of 60 gm.; nearly all Pentelow's fish were however much below this weight. Dawes (1931) found a similar relation between size and maintenance requirement in the plaice (*Pleuronectes platessa*). Brown's data also showed that the maintenance requirement of two-year-old trout increases with temperature, which is in accordance with the general effect of temperature on metabolic processes. The effect of using a constant value for the maintenance requirement in estimating the food consumption of a trout population will therefore probably be to produce an under-estimate during the summer, and particularly the first summer, and an over-estimate, possibly of decreasing magnitude, during the winter. A further complication, the magnitude of which cannot at present be assessed, is introduced by the fact that all the determinations referred to above were made with fish kept in confined quarters with relatively slight current and having their food brought to them. It appears possible that wild fish in a stream, perpetually maintaining their position against the current, and frequently having to quarter the stream bed in search of food, may require considerably more food for maintenance purposes than would the experimental fish. This is suggested by the work of Karzinkin (1939) who found that young pike (*Esox lucius*), fed on very small food-animals so that they had to hunt continuously to obtain an adequate ration, used an increasing amount for maintenance as they grew larger. Estimates of maintenance food requirements based on the experimental data may therefore tend to be below the true value for wild fish.

The efficiency of conversion is also shown by the experimental data to undergo changes which might affect the accuracy of estimates of food consumption which were based on a constant conversion factor. Pentelow's results indicate that efficiency is lower between 50° F (10° C) and 60° F (15.6° C) than it is below 50° F, and that it is lower still at temperatures above 60° F; Brown, on the other hand, found efficiency to be at a maximum of about 8° C and 18° C, and to decline below, between and above these values; the difference between these results may again arise from the fact that one deals with ingested food and the other with assimilated food. If Pentelow's conclusions, which have been shown to be more closely applicable to the present problem, are accepted, then the estimates of food required for growth, based on a constant conversion factor, will tend to be too high in winter and too low in summer. The seasonal inaccuracies due to changes in maintenance requirements and in efficiency of conversion will therefore be in opposite directions, and will tend to cancel each other. None of the published data appear to indicate that the net efficiency of conversion changes with age, and the effect most likely to influence the accuracy of the estimates of food consumption therefore appears to be the change in the maintenance requirement with age. This is likely to lead to under-estimates for young fish and over-estimates for older fish.

TABLE 64. The amount of food, in kg., estimated to have been consumed and utilized for maintenance, growth, and all purposes, by each year-class, in each zone in successive periods between May, 1940, and October, 1941.

Zone.	1940. Oct.–Jan.	1940. Jan.–May.	1940. May–Oct.	1939. May–July.	1939. July–Oct.	1939. Oct.–Jan.	1939. Jan.–May.	1939. May–Oct.	1938. May–July.	1938. July–Oct.	1938. Oct.–Jan.	1938. Jan.–May.	1938. May–Oct.	1937. May–July.	1937. July–Oct.	1937. Oct.–Jan.	1937. Jan.–May.	1937. May–Oct.	1936 & earlier. May–July.	1936 & earlier. July–Oct.	1936 & earlier. Oct.–Jan.	1936 & earlier. Jan.–May.	1936 & earlier. May–Oct.
											YEAR-CLASSES.												
Food Used for Maintenance																							
I ..	71	175	156	86	121	247	309	111	94	166	117	52	34	41	74	52	52	24	39	51	29	16	6
II M ..	26	139	205	119	199	225	285	215	91	78	54	21	17	16	29	19	17	9	8	10	7	4	2
II R ..	5	31	34	27	44	49	64	49	20	16	10	4	4	4	8	6	6	2	3	3	1	1	1
III ..	22	30	38	28	56	69	127	104	79	125	91	40	28	0	0	0	0	0	44	38	11	11	8
IV ..	14	8	43	14	54	75	93	88	33	46	34	16	9	61	69	41	37	15	13	12	5	3	2
V ..	1	6	8	8	19	24	30	40	6	5	3	1	2	3	3	2	1	2	3	2	1	1	0
Food Used for Growth																							
I ..	1380	780	223	299	356	281	92	4	147	76	34	12	0	42	51	21	9	4	0	0	0	0	0
II M ..	886	524	165	369	525	235	101	37	147	37	21	12	4	101	12	9	9	0	0	0	0	0	0
II R ..	207	126	42	76	122	46	21	4	25	9	4	4	0	16	4	4	0	0	0	0	0	0	0
III ..	606	131	71	92	85	198	0	0	104	34	34	34	4	0	0	0	0	0	0	0	0	0	0
IV ..	451	71	138	42	106	97	58	21	34	34	9	9	0	0	0	0	0	0	0	0	0	0	0
V ..	30	25	21	25	34	25	42	0	9	4	4	0	0	0	0	0	0	0	0	0	0	0	0
Total Food																							
I ..	1451	955	379	385	477	528	401	115	241	242	151	64	34	83	125	73	61	28	39	51	29	16	6
II M ..	912	663	370	488	724	460	386	252	238	115	75	33	21	117	41	28	26	9	8	10	7	4	2
II R ..	212	157	76	103	166	95	85	53	45	25	14	8	4	20	12	10	6	2	3	3	1	1	1
III ..	628	161	109	120	141	267	127	104	183	159	125	74	32	0	0	0	0	0	44	38	11	11	8
IV ..	465	79	181	56	160	172	151	109	67	80	43	25	9	61	69	41	37	15	13	12	5	3	2
V ..	31	31	29	33	53	49	72	40	15	9	7	1	2	3	3	2	1	2	3	2	1	1	0

Despite the minor systematic deviations which may occur, it appears that a substantially correct estimate of food consumption by the Horokiwi trout population can be made by this method. The estimated food consumption for maintenance and growth purposes, for each year-class in each zone, is shown in Table 64, for successive periods between May, 1940 and October, 1941. The maintenance food has been estimated at 1.23 per cent. per day of the average stock for the period, the average stock being calculated as the mean of the amounts shown in Table 58 as existing at the beginning and end of the period. The period May to July, 1940 has been included, as in the production data, in order to complete a normal year and so to build up a composite year-class; the mean stock for this period has been estimated by extrapolation. The food required for growth has been estimated at 4.205 times the corresponding amount of production shown in Table 59, since this is the total amount of growth made by all the fish of that year-class in that particular period. The estimated total food consumption is, of course, the sum of these two quantities.

It is evident from the table that at first most of the food is used in production, but that, as the fish grow older, the proportion used for maintenance rises as the

TABLE 65. The percentage used for production in the food eaten during, and in the accumulated amount up to the end of, successive periods in the life of a composite year-class. Results for lower and upper waters shown separately.

	Period Totals.		Cumulative Totals.	
	Lower Waters.	Upper Waters.	Lower Waters.	Upper Waters.
1940—				
October–January	95·8	95·7	95·8	95·7
January–May	80·5	83·6	89·6	94·3
1939—				
May–July	76·2	76·2	87·5	91·7
July–October	73·4	63·6	84·4	86·7
October–January	51·8	65·6	80·2	82·5
January–May	23·4	28·6	74·4	75·7
1938—				
May–July	61·0	55·4	73·5	74·3
July–October	32·0	29·0	72·0	70·6
October–January	24·6	26·9	70·6	68·6
January–May	26·7	43·0	70·3	67·7
1937—				
May–July	72·3	0	70·4	66·5
July–October	38·7	0	69·7	65·4
October–January	30·7	0	69·4	64·6
January–May	19·4	0	68·9	63·8
1936—				
May–July	0	0	68·6	63·0
July–October	0	0	68·1	62·2
October–January	0	0	67·8	61·8
January–May	0	0	67·7	61·5

stock builds up and the growth rate declines. This is still more evident in Table 65 which shows the proportion of food used for growth or production at successive stages in the life of a composite year-class; the zones have again been grouped into the lower and upper waters. The sequence of events is very similar in the two parts of the stream, except that in the upper waters the proportion of the food intake used for production falls earlier to zero as a result of the earlier cessation of growth in this part of the stream. It appears that in a typical year, or in the complete life of a year-class, approximately two-thirds of the food eaten is used for growth and one-third for maintenance.

The amount of food consumed may be considered in relation not only to the fish population which it supports, but also to the source from which it is drawn. The percentage of the total food consumed which is used for maintenance has been shown in Table 65 to be higher in the lower waters (67.7 per cent.) than it is in the upper waters (61.5 per cent..). In Table 66 this percentage, as well as the mean instantaneous growth rates for the first two years, is shown for all the zones, including the two sub-divisions of Zone II. It is evident that there is a

TABLE 66. Comparison for the six zones in a normal year between the mean density of the stock, the density of total food consumption, the percentage of food used for production, the mean instantaneous growth-rate ($\times 10^4$) over the first two years, the average density of the bottom fauna, the density of production of trout and the ratio between the amount of food used for maintenance in the course of a year, and the average density of the bottom fauna. Densities are expressed in gm. per sq. ft.

	Zones.					
	I.	II M.	II R.	III.	IV.	V.
Mean density of stock ..	2·53	3·32	1·14	2·05	3·32	2·09
Density of food consumed ..	34·6	47·6	15·7	24·0	36·9	24·3
Percentage food used for production	66·7	68·9	68·7	63·1	59·2	62·4
Mean growth rate	114	109	109	105	101	106
Density of fauna	0·647	0·417	0·417	0·261	0·236	0·415
Density of production ..	5·36	7·81	2·57	3·59	5·18	3·60
Maintenance food/mean fauna ..	17·8	35·4	11·8	34·0	63·8	22·0

tendency for the proportion of food used for growth to be higher in those parts of the stream where growth is most rapid. Such an effect might have been anticipated whatever the relation between growth and the actual amount of food available. In a previous section, however, the amount of potential food present in the bottom fauna of the various zones has been examined, and it is of interest to compare this also with the results for food consumption and growth. Table 66 therefore shows the average wet-weight density of the bottom fauna in each zone; the figures given are the values shown in Table 20 for 1940 when conditions in the stream were normal. It is obvious that the average stock of the bottom fauna, as represented by these figures, is remarkably low when compared to the amount taken by the trout, which represents the crop of bottom fauna. It has been shown earlier that the food derived by trout from other sources is obtained partly from the surface, which supplies less than 5 per cent. of the total, and partly as small fish, which are negligible during the first two years of the trout's life, and form less than 20 per cent. thereafter. Since about 80 per cent. of the total food of a year-class is taken during these first two years it appears justifiable, particularly

in view of the generally low level of accuracy of the results, to consider the relation between food consumed and bottom fauna as though all the food were derived from this source. The data suggest that there may be a negative relation between the density of the bottom fauna and the amount of food consumed per annum, although the density of the bottom fauna is substantially greater in the Main Water, and particularly in Zone I, than in the Road Branch for the same rate of consumption. It has been shown earlier, however, that in the lower zones, and especially in Zone I, the proportion of forms which are very little eaten by trout, e.g., Parnidae and Oligochaeta, is very much higher than in the upper waters. If these forms are eliminated, the density of the bottom fauna for a given density of food consumption is about the same in both the upper and lower waters.

In all zones the density by weight of the trout population is much greater than that of the bottom fauna population which supports it. The actual ratios vary between 2.7 in Zone II R and 14.1 in Zone IV; if all other species of fish were included in addition to trout, these ratios would probably have to be increased by about 20 per cent. Although generally somewhat higher, these ratios show considerable overlap with those quoted from various sources by Ball (1948) which were all taken from ponds and small lakes, and ranged between 0.97 and 5.10.

The inverse relation between bottom fauna and trout stock which occurs in the Horokiwi suggests that a state of balance may have been reached between the bottom fauna and the trout population; in this case the total quantity of growth made by the trout, i.e., the production, will tend to be limited by the food supply. If it were fully limited, then the amount produced would be negatively correlated with the pressure on the food supply. That this does not actually occur is evident if the density of production of trout as shown in the table is compared with the ratio between the food used for maintenance and the mean fauna. These two quantities show in fact a positive correlation because they are both dependent on the numerical size of the stock; for the four zones of the Road Branch, where the size of the stream is approximately constant, the value of the correlation coefficient r is 0.964, which is greater than that for a probability of chance occurrence of 5 per cent. If, however, the effect of the size of the population on the production rate is eliminated by examining the growth rate of the average individual, it appears that the growth rate during the first two years, which is the principal growing period, may be inversely related to the ratio between the food used for maintenance and the mean fauna. The correlation coefficient for all six zones is — 0.771, which is slightly below the 95 per cent. level of significance. The points for the Main Water zones lie at a rather higher level of growth rate for the same degree of pressure on the fauna than those for the Road Branch zones, but the same general relationship seems to cover all parts of the stream.

Correlation coefficients have been determined for most of the relationships discussed above, and have been found to lie usually between 0.85 and 0.95, being positive or negative as the case may be; thus they are generally in the region of and sometimes exceed the value of 5 per cent. probability of chance occurrence. Since the results under comparison are not direct observations, but are themselves sometimes subject to substantial sampling errors, the probability of chance effects is actually rather higher than the correlation coefficients indicate. The general

consistency of the results, the high level of reliability of some of the basic observations (e.g. growth rate), and the fact that some of the major sampling errors are systematic in their application, all tend however to increase the probable significance of the results.

The data thus indicate that the food supply, as constituted by the bottom fauna, plays an important part in regulating the population of trout in the various sections of the Horokiwi. The limitation on the quantity of food which the trout can obtain from the bottom fauna apparently causes the relative size of the surplus, beyond the maintenance requirement, which can be used for growth, to decrease as the pressure on the food supply rises with increasing stock. As a result the rate of production relative to the stock is reduced by the decreasing individual growth rate. This results in a self-regulating mechanism which tends to maintain the weight of the stock at a constant level by increasing or decreasing growth rate as the stock varies. Such a mechanism is an example of intra-specific competition in the sense in which the term is used by Nicholson (1937) to describe a density-dependent reaction tending to stabilize a population. The immediate reaction in this instance is apparently towards stabilizing the mass of the stock by adjusting the size of individuals by altering the rate at which they grow. A similar stabilizing influence will however also tend to be ultimately applied, although indirectly, to the numerical size of the population. This will be produced through the relation between the size of a female fish and the number of eggs it produces. It has been shown earlier that this relation is apparently independent of the zone in which the fish lives, and therefore presumably of the rate of growth; it has also been shown that the age at which a fish becomes sexually mature is similarly independent of rate of growth. There is, at present, no evidence of any local variations in the rate of mortality between first and subsequent spawnings which might be correlated with rate of growth. The rate of growth will therefore tend to have a direct and substantial effect on the number of eggs produced by a given number of fish, and a decrease in it will tend to reduce the number of individuals produced at the start of a new generation. It is also possible that there might be a further stabilizing influence exerted on the number of individuals comprising the population if the reduced growth rate extended the early period of very high mortality rate and so reduced the ultimate number of survivors. These effects will in turn reduce the pressure on the food supply and so permit of an increase in the rate of growth. Thus the relation between rates of growth and density of stock which appears to occur in the Horokiwi will have a stabilizing effect not only on the mass of the population (the stock), but also on the numbers of individuals.

While it cannot be maintained that the existence of a regulating mechanism of this nature in the Horokiwi trout population has been proved, it appears that, as far as they have been investigated, the relationships between population density, food supply, and growth rate in the various zones vary in the manner which would have been expected if such a mechanism were in operation. The mechanism suggested is also in accordance with what is known as the causal relationships between these quantities. A more directly experimental approach by such means as the artificial variation of the numerical populations of certain zones would

probably be necessary to place the existence of such a system beyond doubt; a higher standard of reliability in the determination of the population densities of both fish and bottom fauna would also be essential.

It is evident from the data in Table 66 that in the various zones the trout populations have stabilized at very different levels of growth rate and density, although in general the relationships in all zones tend to conform to a single pattern and to give a reasonably good fit to a single line. The only significant exception appears to be a tendency for growth rate to be higher in the Main Water than in the Road Branch for a similar trout stock to bottom fauna ratio; even in this respect the relationships between the individual zones within each area seem to be similar and to be along parallel lines. The actual level at which any population becomes stabilized will depend upon the operation of factors which affect the fish population but do not form part of the self-regulating system discussed above. These factors could either be density-dependent and so have, themselves, a stabilizing effect, or their action could be independent of the density of the trout population but could affect the numbers of trout or their rate of growth or the abundance of the bottom fauna.

Hobbs (1940) has suggested that, in New Zealand, trout populations "commonly develop until checked by lack of further spawning-grounds rather than by lack of food." This view is based on the occurrence of a high degree of superimposition among the redds in most of the spawning areas examined, and on the apparent absence of any correlation between the proportion of redds superimposed and the rate of growth of the trout. It has already been shown that in the Horokiwi about 30 per cent. of the redds observed were contiguous with other redds despite the large areas of suitable gravel which were unused by spawning fish, and it has been suggested that this was due to the gregarious habits of spawning fish. While it cannot be questioned that in some waters the area of gravel suitable for spawning is so limited as to have a controlling effect on the population, the gregarious habits of spawning fish would tend to make the proportion of superimposed redds an unreliable index of the limiting action of spawning areas, except in extreme cases. They would also tend to reduce the regulatory effect of superimposition losses by making their extent less dependent on the relative area available for spawning. In the Horokiwi, where there is abundant suitable gravel, it seems unlikely that the regulatory effect of the available spawning area has importance comparable with that of the food supply; although the losses caused by the displacement of eggs by subsequent spawners will have some effect on the level at which the population is stabilized.

The data give more support for the existence of factors directly affecting growth rate although they do not suggest their method of operation. It has already been pointed out that in the Main Water the trout tend to grow relatively more rapidly in relation to density of stock and food supply, and that this is in agreement with the wide-spread belief that the growth rate of fish has a positive relation with the size of the water. The increased growth rate in Zone V when compared with Zone IV is in accordance with the density relationships, but the fact that this zone shows a noticeable similarity to the Main Water in physical

features (except size) and in the composition of the bottom fauna, suggests that the physical nature of the environment may play a part in determining the levels of growth rate and density at which the trout population is stabilized.

Although the amount of food available apparently has a limiting effect on the trout stock of the Horokiwi, it seems unlikely that competition for food with other species of fish, except possibly eels, is of any great importance in this connection. The native fish population of Zone I is at all times very much greater than that of any other zone, and this zone should therefore be most likely to show effects on trout production due to these fish. Both the rate of growth of trout and the density of the bottom fauna are however relatively high in relation to the density of the trout stock, while inter-specific competition might be expected to produce the opposite effect. If effects due to the small native fish are not apparent in the zone where they are most abundant, it is unlikely that they are of importance in other sections of the stream. The limited data available suggest that eels are more or less equally abundant in all parts of the stream, and therefore local effects on the trout due to their presence cannot be expected.

In the discussion of the bottom fauna it was pointed out that most of the common invertebrates showed the same type of variation in average size in different parts of the stream, and it appeared later that this closely paralleled the local distribution of the growth rate of trout. Such a pronounced similarity is unlikely to be due purely to chance, and, although the data are inadequate for a definite explanation, two hypotheses appear possible. The similarity could arise through the operation of environmental factors which affected in a parallel manner the rate of growth of trout and of most of the invertebrates. It could also arise from the inverse correlation between trout growth rate and density of stock, if the effect of increased predatory pressure by the trout were to remove more of the larger individuals from the bottom fauna, and so to depress the average size. That the second hypothesis is not very probable is suggested by the fact that the two Sericostomatidae, *Pycnocentrodes* and type "C," which are freely eaten by trout only when large, show the normal size distribution in the stream, even at seasons when the larvae are all too small to be eaten by the trout. On the other hand, it is interesting to note that the only abundant and homogeneous group which is very little eaten, the Parnidae larvae, is also one of the few which show little local variation in size. It is clear that much more investigation into the origin and nature of the local variation in the mean size of the invertebrates is required, and it is not impossible that such an investigation would throw further light on the causes of local variations in the growth rate of trout.

Although the data suggest that the supply of food plays an important part in determining the growth rate of trout in the different zones of the Horokiwi, it does not seem likely that this effect could be readily shown by differences in the amounts of food present in the stomachs of trout taken from the different zones. In Zone I where the growth rate is greatest the average size at the end of the first year (165 gm.) exceeds that in Zone IV where the growth rate is at a minimum (70 gm.) by 136 per cent., but the average instantaneous growth rate over the year (0.0203) is only 13 per cent. greater than in Zone IV (0.0180). If these figures are applied to the regression line relating growth rate and food

consumption, the average daily consumption in Zone I is found to be 9.76 per cent. of feeding weight per day, which is only 11 per cent. greater than the figure of 8.80 per cent. for Zone IV. It seems improbable that there would be any difference in the rate of digestion in the two zones under otherwise similar conditions, and the average amount of food found in the stomachs of fish in Zone I should therefore be expected to be about 11 per cent. greater than in Zone IV. It has been shown earlier that in collections of fish taken under uniform conditions, the normal variation is such as to give a range for the 95 per cent. limits of probability of the mean of about ± 22 per cent. where the samples were of the size usually taken in this work. The differences in the average amounts of food taken by fish in Zones I and IV are not therefore large enough to be shown by the data at present available. It can be shown that the samples would have to consist of at least 100 fish for a difference of 11 per cent. in the means to have 95 per cent. probability of significance. The amount of food in the stomachs of fish is also subject to much larger variations induced by several causes other than those producing the local differences in growth rate. The causes of these variations include those associated with changes in the growth rate due to increasing age and to seasonal effects as well as temporary influences such as floods, and it would therefore be necessary to ensure that the samples were strictly comparable in all these respects before effects due to local growth rate differences could be demonstrated. Frost (1939 and 1945) has compared the amounts of food found in the stomachs of trout taken in two sections of the River Liffey, where the growth rates are very different, with rather inconclusive results. When the average amount of food, expressed as a percentage of body weight, in the stomachs of fish of all sizes, was compared, there was a slight tendency for there to be more food in the stomachs of the fish from the slow-growing area, but when the actual amounts in the stomachs of fish weighing less than 150 gm. were compared, a greater amount was found in the fish from the area of rapid growth. This latter effect might be due to the fact that fish of the same size were younger in the area of rapid growth, since the instantaneous growth rate and the amount of food evidently decline as the fish grow. The average amount of food recorded by Frost is substantially greater than that found in Horokiwi trout of similar size. There are however at least three differences in the nature of the data which might contribute to this effect. Frost's fish were all rod-caught, which may have led to some selection of actively feeding fish; Frost's data are based on the actual wet weight of the stomach contents, while the Horokiwi data are back-calculated from the dry weights, so that the former may include a greater weight of gastric secretions than the latter; the Horokiwi data also exclude the weights of the shells and cases of molluscs and Trichoptera which are included in the other weights. The first two of these differences might, and the third certainly would, cause the Horokiwi weights to be below those obtained in the Liffey.

It is evident from Table 66 that the amount taken by the trout during one year exceeds by many times the total weight of bottom fauna present at any one time. Further information on this aspect may be obtained if the data are considered on a numerical rather than a weight basis. For this purpose it is necessary to consider

TABLE 67. The mean instantaneous growth-rate (x 10^4) and relative weight of stomach-contents (in % body-weight), both smoothed with a running mean of 3; the estimated daily food consumption (in % body-weight), the ratio of daily consumption to stomach-contents, and the monthly mean temperature (°C.). Results by months for the 1939 year-class.

	Growth-rate.	Stomach contents.	Estimated Daily Consumption.	Consumption/Contents Ratio.	Mean Temperature.
1939—					
November	369	1·21	16·73	13·8	16·0
December	302	1·07	13·91	13·0	17·9
1940—					
January	253	0·82	11·86	15·9	19·5
February	207	0·76	9·93	13·1	16·9
March	185	0·68	9·00	13·2	16·2
April	111	0·60	5·89	9·8	12·8
May	59	0·52	3·71	7·1	11·2
June	42	0·48	3·00	6·3	8·2
July	56	0·42	3·58	8·5	7·5
August	56	0·38	3·58	9·4	10·2
September	54	0·31	3·50	11·3	11·5
October	39	0·25	2·87	11·5	13·6
November	47	0·25	3·21	12·8	16·0
December	36	0·19	2·74	14·4	17·9
1941—					
January	36	0·19	2·74	14·4	19·5
February	19	0·15	2·03	13·5	16·9
March	23	0·15	2·20	14·6	16·2
April	27	0·13	2·37	18·2	12·8
May	20	0·13	2·07	15·9	11·2
June	19	0·14	2·03	14·5	8·2
July	12	0·16	1·73	10·8	7·5

further the relation between the amount of food found in the stomachs of fish and the total daily consumption. It has already been shown that the daily consumption can be computed with reasonable accuracy from the rate of growth, and detailed results of the variations from month to month in the rate of growth and the amount of food in the stomachs of the 1939 year-class have already been presented. This relation is examined further in Table 67. This shows for each of the 21 months from November, 1939 to July, 1941 the mean instantaneous growth rate and mean proportionate amount of food in the stomachs of the 1939 year-class. The data have been taken from Tables 44 and 52 respectively, and in order to reduce chance irregularities, both sets have been smoothed with a running mean of three. The average daily food consumption has been determined by applying the growth rates to the regression line developed above. The fourth column shows the ratio between the daily food consumption and the mean stomach contents. It is obvious that this shows seasonal changes, and a further basis for comparison is given by the mean monthly temperatures, which have been taken from Table 16. This comparison is illustrated in Fig. 21, which shows that, despite the great variations in the rate of growth, the consumption:stomach-contents ratio varies very closely with temperature up to March of the second year. At this

time the ratio appears to rise abruptly; thereafter it varies again with temperature, although at a higher level than before. This relationship is probably mainly due to the effect of temperature on rate of digestion. This has been directly investigated by Markus (1932), working with the black bass (*Huro floridana*), who found that the rate of digestion varied even more rapidly with temperature than it does in the present instance. Leonard (1942) has drawn attention to the very slow rate of digestion in trout at low temperatures. It is of interest that over the limited range of temperatures observed the data shown in Fig. 21 conform closely to a very usual effect of temperature on chemical reactions in that a 10° C rise of

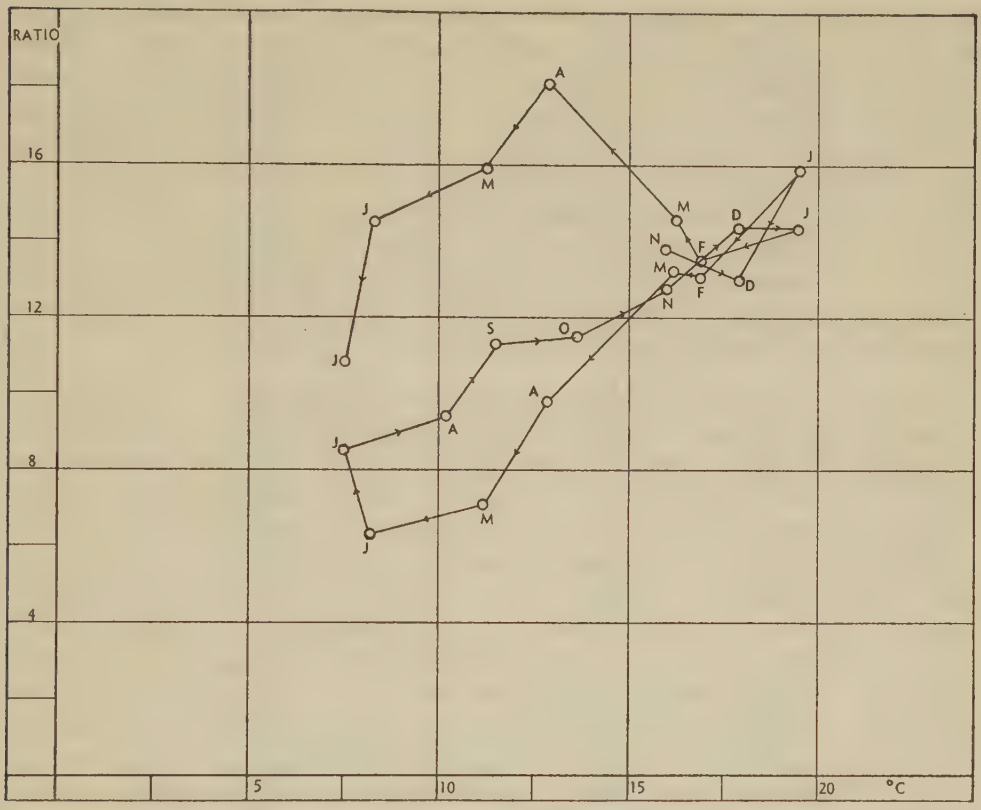

FIGURE 21. The ratio between estimated total daily food consumption and mean stomach contents, plotted for each month against mean water temperature, for trout of the 1939 year-class. The points are marked with the initial letter of the appropriate month and consecutive points are joined by arrows.

temperature appears approximately to double the rate of digestion. The relation between temperature and the consumption : stomach-contents ratio will also be affected by the influence of temperature on the maintenance ration and on the efficiency of conversion; it has been shown however that these two effects probably tend to cancel each other. The rather aberrant nature of the results for the last four months may simply be due to chance effects arising from the limited material available for this period; but in view of the consistency of the results and the apparent re-establishment of a normal temperature relationship it seems possible

that it is due to physiological changes connected with the development of sexual maturity in the fish at this time. Insufficient data regarding the growth rate of the year-classes earlier than 1939 are available to enable additional comparisons to be made.

It has been shown earlier that trout probably do not feed freely in the later part of the night. In this case the total daily food requirements have to be taken in a period of about 18 hours, and the actual rate of digestion is about one-third higher than the consumption : stomach-contents ratio indicates.

There appear to be few other data with which to compare the conclusion that the ratio of daily consumption to mean stomach contents varies between 7 and 16 according to temperature. Ricker (1937) found that at 12.0° C half of a sample of young sockeye salmon fed on entomostraca had completely emptied their stomachs in 4 hours, and that the average stomach contents was reduced to less than 10 per cent. of the original value in that time. This suggests a rate of digestion not greatly below that found for Horokiwi trout at the same temperature, and in further discussion (Ricker and Foerster, 1948) the same author considers that a value of four to one is the most probable estimate of the ratio of daily food consumption to stomach contents. This is probably about half of the value obtained for trout at a similar temperature in the present study, but in view of the indirect nature of the evidence in both cases the agreement is reasonably close.

The ratios which have been determined between the amount of food in the stomachs of the fish and the daily food consumption can be used to make approximate estimates of the number of food organisms eaten in a day. This may be estimated as the product of the consumption : stomach-contents ratio and the average number of organisms found in the stomachs of the fish. An error will occur, due to the fact that all recognizable animals will be counted in full, although most of them probably only contribute a part of their original weight to the stomach contents. This error will tend to lead to an over-estimate of the number of food-animals eaten daily, but its extent cannot be determined without much more detailed knowledge than is at present available concerning the processes of digestion. If a food-animal undergoing digestion loses weight at a constant rate, and remains recognizable up to the final moment of disappearance, the estimate would tend to be about double the correct value. This can probably be taken as the maximum limit of the error, and therefore the estimates based on direct multiplication of the average number of animals in the stomach and the consumption : stomach-contents ratio are likely to be somewhat greater than, but not more than twice, the true values. The estimated numbers of animals consumed in a day are set out in Table 68; the data for the year-classes older than 1938 have been grouped together to obtain satisfactory samples, and the few fish of these year-classes taken after January, 1941 have been omitted. The ratios used in the conversion are those given for the 1939 year-class in Table 67; for the fish of the pre-1939 year-classes, the second-year ratios for the 1939 year-class in the corresponding month have been used. Fish from all zones have been grouped together in this table since no significant difference could be found at any period between the fish from the lower and upper waters despite their differences in size. The small differences which did

occur generally led to a greater average number of food organisms being found in the smaller fish of the upper waters.

TABLE 68. The average number of animals found in the stomachs of the 1939 year-class and older fish in each month and the estimated number eaten per day.

Year-class.	Month.	No. of Fish.	Average No. in Stomachs.	Estimated Daily Consumption.
1939	1939—			
	November	57	7·7	106
	December	2	23·5	305
	1940—			
	January	20	16·4	261
	February	22	36·1	473
	March	3	34·3	452
	April	25	33·3	326
	May	9	33·3	237
	June	..	..	..
	July	26	53·1	451
	August	12	68·5	644
	September	24	102·1	1,164
	October	19	83·0	955
	November	19	117·2	1,500
	December	22	177·7	2,555
	1941—			
	January	20	97·4	1,402
	February	22	26·7	360
	March	19	56·5	824
	April	7	24·7	449
	May	7	47·9	761
	June	11	57·0	827
	July	5	12·4	134
	August	..	..	..
	September	12	83·2	1,064
	October	7	41·3	570
1938 and earlier	1940—			
	July	16	75·0	646
	August	3	103·0	970
	September	10	150·0	1,690
	October	8	177·0	2,040
	November	10	109·0	1,395
	December	12	207·0	2,980
	1941—			
	January	7	42·0	605

The data for daily food consumption have been combined with those given in Table 30 for the number of fish of each year-class present at various dates, to give an estimate of the total number of food-animals eaten by the trout population. These estimates are developed in Table 69. The number consumed per day by an individual fish is taken from Table 68; the values for the 1940 year-class are taken to be the same as for the 1939 year-class at the same age; the mean for October–January for the 1940 year-class has been fixed rather below the true mean on account of the great decrease in numbers which occurred during this

period. The population data have been taken from Table 30; the period means are the geometric means of the estimated population at the beginning and end of each period; geometric means have been used because the population generally appears to be decreasing logarithmically. The total consumption is the product of the estimated consumption by one fish during the period and the mean population; the cumulative total covers the comparatively normal year from May, 1940 to May, 1941 and gives the progressive consumption by a composite year-class in the same way as was done for production and for food consumption by weight.

TABLE 69. The estimated number of food organisms eaten by a fish in a day, the mean population and estimated total number of food animals consumed in each period between May, 1940, and May, 1941; also the cumulative totals for a composite year-class. Results are shown separately for each year-class and for the upper and lower waters.

Year-class.	Period.	Lower Waters. No./fish /day.	Mean Population.	No. Consumed. ($\times 10^6$)	Cumulative Consumption. ($\times 10^6$)	Upper Waters. No./fish /day.	Mean Population.	No. Consumed. ($\times 10^6$)	Cumulative Consumption. ($\times 10^6$)
1940	Oct.–Jan. ..	150	57,800	930	930	150	10,500	169	169
	Jan.–May ..	400	7,620	365	1,295	400	1,780	86	255
1939	May–July ..	305	4,420	82	1,377	305	1,260	23	278
	July–Oct. ..	835	2,490	191	1,568	835	1,560	120	398
	Oct.–Jan. ..	1,743	2,015	323	1,891	1,743	1,280	206	604
	Jan.–May ..	679	1,515	121	2,012	679	1,070	87	691
1938	May–July ..	765	780	36	2,048	765	895	42	733
	July–Oct. ..	1,333	540	66	2,114	1,333	710	89	822
	Oct.–Jan. ..	1,932	375	67	2,181	1,932	380	68	890
	Jan.–May ..	679	100	8	2,189	679	140	11	901
1937	May–July ..	765	130	6	2,195	765	190	9	910
	July–Oct. ..	1,333	170	21	2,216	1,333	255	32	942
	Oct.–Jan. ..	1,932	105	19	2,235	1,932	165	29	971
	Jan.–May ..	679	70	6	2,241	679	110	9	980
1936	May–July ..	765	32	2	2,243	765	125	6	986
	July–Oct. ..	1,333	9	1	2,244	1,333	85	11	997
	Oct.–Jan. ..	1,932	4	1	2,245	1,932	33	6	1,003
	Jan.–May ..	679	4	0	2,245	679	28	2	1,005

The amount consumed in each part of the stream may be compared with the normal bottom fauna population. Although the methods used for sampling the bottom fauna may have led to the incomplete recording of very early instars of some insects it is believed that virtually complete counts were obtained of all larvae which had reached the minimum size eaten by fish (about 2 mm.). The data are therefore satisfactory for quantitative comparison between the bottom fauna and food consumed. If the area of the stream bed is multiplied by the mean numerical densities of the bottom fauna for 1940 shown in Table 20, the estimated total bottom fauna of the lower waters is found to be 132 million animals, and that of the upper waters to be 58 million. The estimated annual consumptions of 2245 million and 1005 million animals are therefore 16.9 and 17.3 times the normal population respectively. These ratios are very much smaller than those between the weights of bottom fauna present and consumed; the difference probably arises from the tendency of the trout to eat only the larger individuals of the various species.

Both the numerical and weight ratios are based on comparison of the total quantities of all forms in the bottom fauna, and in the food of the trout. It has been shown however that there are great differences in the extent to which the various animals are eaten, and consequently, for any particular form, the ratio between stock and annual consumption by trout may differ widely from the average value. *Delcatidium* nymphs form the main source of food of trout in their first year, the

average percentage in the food for the first nine months being nearly 85 per cent. (Table 46). In older trout *Deleatidium* forms rather less than 20 per cent. of the food. An approximate estimate of the total annual consumption of *Deleatidium* may be made by taking five-sixths of the food-animals eaten by trout in the first nine months, and one-sixth thereafter. This gives a total of 1645 million *Deleatidium* eaten in a year. An approximate estimate of the standing population of *Deleatidium* is one-sixth of the total bottom fauna population, i.e., 32 million. Thus, the annual consumption of *Deleatidium* is about 50 times the average stock; most of these are taken as well-grown nymphs, but in spring and early summer the newly-hatched fry are feeding upon relatively small nymphs. This is probably the highest ratio for any of the important animals in the bottom fauna. The other animals with high forage ratios are either eaten only for a short time when the trout are small, e.g., Chironomidae and *Paracalliope*, or else only by large trout, and then often seasonally, e.g. Sericostomatidae. The ratio between consumption and population for the Sericostomatidae will be reduced both by the limitation of predation to large larvae and by the relatively high proportion of the fauna which these animals form in all but the lowest parts of the stream. It can be shown by the methods used above that the combined ratios for the three Sericostomatidae which show seasonal changes are respectively about 15 and 3.5 for the lower and upper waters. At the other extreme, the annual consumption of such animals as the Parnidae and Oligochaeta is probably less than their normal standing population.

In these comparisons estimates have been made of the amount of bottom fauna which is consumed by the trout. The total bottom fauna production in a year must include, in addition, the individuals dying from natural causes, the individuals reaching maturity and leaving the water and not returning, the individuals with a life-cycle of more than one year who survive into the following year, and the individuals eaten by predators other than trout. Most of these other predators are also fish, but we have seen that, except for the eels, these are only numerous in Zone I and, on account of their small size, their total mass is probably unimportant compared with the trout stock. The eel population has not been measured but the density of the stock is probably about 30-50 lb. per acre, and is therefore only 15 per cent. to 20 per cent. that of the trout, and on account of its relatively slow growth rate, the quantity of food consumed by the eel will probably be an even smaller proportion of that eaten by the trout. In its later stages the eel feeds largely upon smaller fish and it is therefore not fully competitive with the trout as a predator on the bottom fauna. The trout therefore is probably the principal predator on the bottom fauna. Even so, it appears that the total annual production of the bottom fauna as a whole must be well over 17 times that of the average stock on a numerical basis, or 100 times on a weight basis, while the ratios of some of the most freely eaten forms, particularly *Deleatidium*, must be up to three times as great.

Very few similar data are available with which these ratios may be compared. Borutzky (1939a and b) carried out a detailed study of production in the bottom fauna of Lake Beloie. From his results it appears that the average population of the dominant form (*Chironomus plumosus*) was about 210 million individuals, weighing about 780 kg. During one year aquatic predators took about 116 million

weighing about 440 kg. In this case the crop is only about 61 per cent. by number, or 56 per cent. by weight, of the average stock. For the entire bottom fauna the proportion was even lower, the weight of all significant forms taken by predators being only 32 per cent. of the average stock.

Somewhat similar studies have been made on the chironomid fauna of Costello Lake in Canada by Miller (1941). In this case the mortality among older larvae was found to be about 50 per cent. in deeper water but, since there appeared to be two or three complete turn-overs in a season, the mortality would amount to about one to one and a half times the normal population. In shallow water the rate of turn-over was greater, but the mortality was proportionately much less. Since, however, no observations were made on the rate of mortality among young larvae, or upon the fraction of the mortality which was due to predation, the results cannot be closely compared with the Horokiwi data.

Mortality in the Ephemeroptera population of a rapid stream has been studied by Ide (1940). In three species of *Leptophlebia* the survival from egg-production to hatching of subimagines ranged from 0.19 per cent. to 0.44 per cent., so that the total mortality must be very many times the final population of nymphs. It seems not improbable however that much of this mortality arises from eggs which are not successfully deposited, or which otherwise fail to give rise to surviving larvae, and it is not possible therefore to obtain even an approximate figure for mortality among the older larvae which would be most subject to predation.

In comparison with these figures the annual consumption of bottom fauna by trout in the Horokiwi seems remarkably high in relation to the size of the bottom fauna stock. Although some of the quantities on which the estimate is based are subject to considerable sampling errors, there can be no doubt that the amount consumed is many times the average stock of bottom fauna. The basic quantities involved are:

(a) The density of the bottom fauna, which has been shown to be similar to that of many other trout streams in various parts of the world;

(b) The area of the stream bed, which is subject to very little error;

(c) The daily food requirement of a trout, which is derived from the results of several other workers, all in good agreement, and from the growth rate of trout in the Horokiwi, which, although unusually high, has very small probable errors;

(d) The stock of trout, which is based on estimates of population which, although they are higher than in most other waters studied and have large probable errors, are in good agreement with the estimates of catch made independently. Even if the maximum errors which appear likely were allowed for, the ratios under discussion would only be reduced by half and would therefore still be very high compared to the data for other waters.

Ide (1940) has pointed out that the number of *Leptophlebia* subimagines rising into tent-traps was greater than the apparent number of mature nymphs in comparable areas of stream bed, and has drawn the conclusion that stream bed sampling gives an incomplete record of the real density of the fauna. While such an effect

would go some way towards explaining the remarkable divergence shown by the Horokiwi data, this conclusion is based apparently on a very small number of comparisons, and it does not appear that any of the standard methods which have been described by various workers were used by Ide in making the faunistic collections.

The amount of food which may be consumed by any link in a food-chain is limited, in a stable state, by the amount produced in the next lower link. This bears no fixed relation to the average stock of food animals over a given period, but depends primarily on the average length of life of each individual, although it is also affected by the shape of the growth curve. Where predation is heavy, so that many individuals are destroyed early in life, the stock will be kept at a relatively low level compared to production and to crop. Even if the life-cycle is annual, a fairly constant stock at a relatively low level could be maintained under heavy predation if breeding were more or less continuous. It seems not unlikely that *Deleatidium* fulfils these conditions since, although many of the species have annual life-cycles (Phillips, 1930), the hatching season of some species covers several months, and the Horokiwi is inhabited by a number of species, which hatch at different seasons. This does not however apply to the three species of Sericostomatidae which are only eaten seasonally, i.e., *Helicopsyche*, *Pycnocentrodes* and type "C," since these have been shown to be single-brooded, to have a fairly short hatching season, and to be eaten only when almost mature. Despite this, the quantity of these larvae eaten by the trout seems to be distinctly greater than the average population. It is obvious that much more detailed investigation of these relationships is required, not only to establish the ratios between stock and crop of bottom fauna beyond question, but also to elucidate the controlling factors in the relationship.

6. EFFICIENCY OF UTILIZATION

(a) Bottom Fauna to Angling Crop

In the preceding sections estimates have been developed of some of the major quantities concerned in the food-chain in the Horokiwi stream. These estimates make it possible to examine the efficiency with which matter is being transferred from one step to the next in the part of the food-chain which has been studied. This part comprises a section such as that shown in Fig. 14, the central organism being the trout. In the present study only the material relationships have been considered, and no attempt has been made to convert them into energy equivalents.

The first quantity for which an estimate is available is the amount of food entering this section of the chain. This is nearly all derived from the bottom fauna, but we have no indication of the proportion of the bottom fauna production which it represents. As Fig. 14 shows, the food ingested can be dealt with in one of three ways. It can be passed through the fish without assimilation; it can be broken down to provide the energy required for maintenance, or it can be converted, with losses, into additional fish material. It is this last fraction only which actively contributes to the production of the next link, the trout. No new data are available from the present study concerning the proportion of food not assimilated, and this must be regarded as being proportionately distributed between the fractions used for maintenance and growth; it probably represents a loss of about 10–20 per cent. in

most cases (Ricker, 1946). The proportions of the food intake which have been used for growth and for maintenance at various stages in the life of the trout have been shown in Table 65.

The proportion used for maintenance increases rapidly during the early part of the life-cycle of a generation as the stock builds up and the instantaneous growth rate decreases. In consequence, the proportion of the total food consumption which has been used in the production of trout decreases during the life of the generation, at first rapidly and then more slowly. The final value is about 68 per cent. in the lower waters and about 61 per cent. in the upper waters, and this proportion apparently decreases as the density of the stock increases.

The efficiency of conversion into trout material of that part of the food which is used for maintenance has to be taken to be 23.8 per cent., following the work of Pentelow and others. Consequently, the amount of trout which has been produced by the end of the life of a generation is only about 16 per cent. and 15 per cent. in the lower and upper waters respectively. At the end of the second year the corresponding figure for both areas is about 17 per cent. of the total food consumed up to that time.

Mortality is continuous from the commencement of the life of a year-class, so that the weight of the stock is never fully equal to the quantity of trout which has been produced. The proportion of the production which is surviving as the stock at any time in the life-cycle has been plotted in Figs. 15 and 16. This value is of course finally zero, but it is at a maximum early in the second year when 30–35 per cent. of the amount so far produced is still surviving; after this time the surviving percentage falls off rapidly. The resulting changes in the proportion of the total food intake which is embodied in the surviving stock are shown in Table 70; the maximum value in both the lower and upper waters is 7–8 per cent.

TABLE 70. Comparison between the total amount of food consumed, the existing stock and the total crop taken to successive points in the life of a composite year-class (all in kg.). Results for lower and upper waters shown separately.

Age-group	0.	I.		II.		III.		IV.	
	May.	Oct.	May.	Oct.	May.	Oct.	May.	Oct.	May.
LOWER WATERS—									
Accumulated consumption	4,350	6,693	8,648	9,554	9,899	10,297	10,501	10,616	10,674
Stock	346	371	339	251	39	71	40	3	3
Percentage stock in food	7·9	5·5	3·9	2·6	0·4	0·7	0·4	0·03	0·03
Crop	0	0	21	21	87	87	107	107	111
Percentage crop in food	0	0	0·24	0·22	0·88	0·84	1·02	1·01	1·04
UPPER WATERS—									
Accumulated consumption	1,395	1,958	2,796	3,309	3,584	3,720	3,801	3,913	3,945
Stock	41	148	203	176	29	42	19	14	9
Percentage stock in food	2·9	7·5	7·3	5·3	0·8	1·1	0·5	0·4	0·2
Crop	0	0	0	0	0·5	0·5	3·5	3·5	5
Percentage crop in food	0	0	0	0	0·01	0·01	0·09	0·09	0·13

Cropping of each year-class begins during its second summer in the lower waters, and during the third summer in the upper waters. It is very light during these years, and it is not until the following seasons, the third and fourth summers respectively, that the population is fully subject to cropping. By the beginning of these seasons the stock has decreased considerably from its maximum, and is equal to 15.4 per cent. and 7.3 per cent. respectively of the total amount produced up to

that time in the lower and upper waters. It is only equal to 2.6 per cent. and 1.1 per cent. of the amount of food which has been consumed up to that time.

These figures would represent the efficiency with which the trout were converting the food into the crop if all the surviving fish were harvested as soon as cropping began. This however is not the case; cropping is carried out by the comparatively inefficient and uncertain process of angling, and is largely limited by the amount of angling effort exerted. This is normally very much greater in the lower waters than in the upper waters, and in consequence the proportion of the stock remaining at the commencement of cropping, which is ultimately removed by angling, is considerably higher in the lower waters. It is here approximately 44 per cent., as against 12 per cent. in the upper waters. These figures include the small quantity of trout taken in the season before their year-class was fully available to anglers, so that they express the total crop, whenever taken, as a percentage of the stock at the beginning of the first full cropping season. It follows from these results, and from those developed in the previous paragraphs, that the crop is only equal to 1.04 per cent. and 0.13 per cent. respectively of the total amount of food consumed in the lower and upper waters. Table 70 shows how the relation between food consumption, stock, and crop changes during the life of a generation. The data are for the composite year-class which has been used in previous tables. A graphical representation of the relation between food consumption, utilization, trout production and crop in the lower waters is given in Fig. 22.

The proportion of the total food consumption which reaches the successive stages in the food-chain may be summarized in the following table:

	Lower Waters.	Upper Waters.
Food intake	100%	100%
Used in growth	68%	61%
Embodied in trout at any time	16%	15%
In trout stock when cropping begins	2.6%	1.1%
In crop	1.04%	0.13%

Although these percentages are subject to the sampling errors in some of the quantities involved, they are probably sufficiently accurate to provide a good indication of the approximate proportions of the original food intake which contribute to the successive stages of the production and cropping of the trout population, and to show that the crop forms only a very small proportion of the original food consumed. It is of interest, and, potentially, of practical importance, to consider some of the factors determining the efficiency of the successive steps, and to examine how far these are, or could be, modified by man's conscious efforts to increase the crop of trout.

The basic quantity, in that part of the chain which has been studied, is the quantity of food consumed by the trout population. This is a function of at least two important factors, the rate of production of the source of food, in this case the bottom fauna, and the intensity with which it is cropped by the trout, which is affected by the density of the trout stock. Attempts to increase the yield to anglers

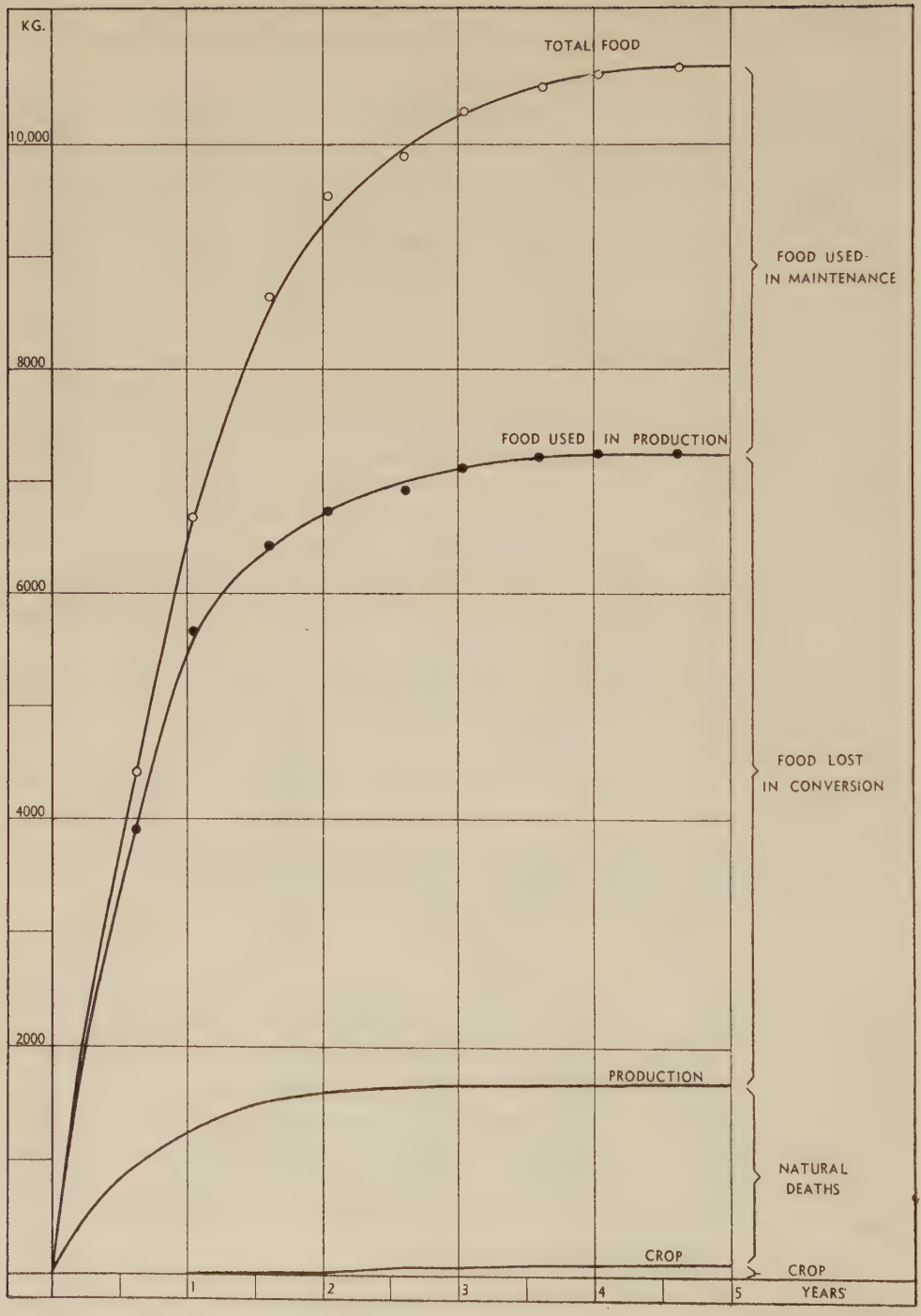

FIGURE 22. Comparison, during the life of a composite year-class in the lower waters, between the total food consumption, the amount of food used in production, the weight of trout produced, and the angling crop.

from a trout population by increasing the amount of food consumed by the population could be directed towards increasing either the rate of production of the bottom fauna or the efficiency with which it is cropped by the trout. The efficiency of cropping can only be increased if the existing predation pressure on the bottom fauna is below the level which gives the maximum sustained yield. Under these conditions the efficiency of cropping, and hence the total food consumption, could be increased by raising the numerical strength of the trout population by such means as artificial liberations. The evidence has indicated that in the Horokiwi the food supply has a stabilizing effect on the trout stock, and that where the trout stock is most dense the bottom fauna is reduced. This suggests that, under the conditions prevailing during this study, the food consumption of the trout was approaching the limit which the bottom fauna production could support. Little benefit can therefore be expected from attempts to increase the yield to anglers by liberations. The amount of stocking which has usually been done in the Horokiwi in the past, about 15,000 fry per annum, has been so small compared to the natural production, about 800,000 per annum, that it is unlikely to have had any significant effect in either direction upon the stock. Even the record liberation of 30,000 fry made in 1941 was insufficient to prevent a very weak year-class occurring due to the destruction of naturally produced eggs and fry by floods. There seems a greater possibility that the food consumption of trout could be increased in a stream such as the Horokiwi by raising the production level of the bottom fauna. Possible methods of doing this would be to increase the food supply of the bottom fauna and to reduce the losses from floods by increasing the stability of the streambed. The first of these objects might be effected by promoting plant growth by adding nutrient salts to the water, the second would call for modifications to the banks and drainage area of the stream. While theoretically possible, both these courses might require action on a larger scale than would be warranted by the increased crop of trout. In any case they are concerned with a section of the production chain which lies outside the scope of the present study, and much additional basic research would be necessary before the possibilities of such methods could be assessed.

About two-thirds of the food intake is actually used to promote growth, and it appears that, in the Horokiwi, this proportion decreases as the density of the stock increases. In these circumstances the only means of improving the efficiency of this step, which is basically dependent on the physiology of nutrition and growth, appears to lie in reducing the stock. The artificial increasing of the stock by liberations would probably have the effect, if on a sufficiently large scale, of reducing the proportion of the food intake which can be used for growth. Since, as we have seen, it is unlikely to lead to greatly increased food consumption, it might actually result in a reduction rather than an increase in production. While the opposite process, the deliberate reduction of the stock by some form of culling, might lead to greater efficiency at this stage, it would be necessary to ensure that it was not taken so far as to bring about a reduction in food intake, and so in the final amount of trout produced. Much further and more accurate quantitative investigation is

needed before the nature of this balance can be determined with sufficient accuracy for practical purposes.

The efficiency of the next step, the conversion into trout material of the part of the food intake actually available for growth, depends entirely upon the physiology of the fish, and while it may be affected by such factors as temperature, and may possibly vary to some extent with amount of food consumed, it would appear to be virtually beyond the control of fisheries management techniques.

The efficiency of the next step in the process of conversion of trout food into angling catch depends upon the continuously changing relationship between the quantity of trout which has been produced and the surviving stock. It is this step which is the most susceptible to modification by appropriate management techniques. It is also this step which shows at present the lowest efficiency. The problem may be approached in two ways. The efficiency of the step could be modified within the present production-stock relationship, or the nature of the relationship itself could be changed. At the moment we are not concerned with the proportion anglers take from the stock which has survived until cropping commences. The problem is therefore to determine the conditions under which the stock would be cropped when at its maximum level. The simplest solution to this problem is that provided by the determination of the time at which the stock curve for any year-class is at its peak. This is a method which has been put forward by Russell (1942) and others, and is particularly applicable to heavily exploited marine fish. Table 63 shows that this point occurs early in the second summer in the lower waters, and during the second winter in the upper waters. The stock will be at its maximum at the time when the average instantaneous growth rate, which is tending to decrease throughout the life of the fish, first falls below the instantaneous mortality rate. Comparison of the smoothed instantaneous growth rates, given in Table 67, and the data on mortality rates given in a previous section, shows that about January of the second year the mortality rate rises from about 0.0035 to about 0.0049, while at the same time the growth rate passes from values of 0.0036 and above to values always below 0.0030, thus crossing the mortality rate. This method, based on combined results for all zones, has thus given a date intermediate between those found by the "stock" method for the lower and upper waters of the stream. A refinement of this method, introduced by Ricker (1945), enables the point of commencement of cropping to be adjusted to give the maximum yield when cropping is a continuous rather than an instantaneous process. Under these conditions, the date of first cropping must always be earlier than that of maximum stock; the difference depends on the relative magnitudes of the natural and angling mortality rates, and increases as the relative natural mortality rate increases. In the simple case considered by Ricker the entire year-class is assumed to pass the size-limit simultaneously, but precise computation of the optimum cropping point is more complex where, as in the present case, an important amount of cropping may take place at a time when part of the year-class is above and part below the size-limit. More accurate knowledge of the relation between natural and angling mortality rates than is at present available is also necessary for the application of this method. All that can usefully be done at present is therefore

to note that when cropping is continuous rather than instantaneous the optimum time for its commencement is rather earlier than the date of maximum stock.

The methods referred to above enable the optimum point of first cropping to be fixed approximately, provided that growth rates and natural and angling mortality rates remain unchanged. An increase in cropping rate will however modify the shape of the stock and cumulative production curves; the production curve will tend to be levelled off at the cropping point, and the stock curve will tend to be cut off at the same point. The data available are sufficient to provide some indication of the effect of such changes on the optimum point of commencement of cropping. This may be considered first on the assumption that the total annual production, which in a steady state equals the total production of a year-class, is constant. Under these conditions, flattening off the top of the production curve will tend to raise its level at all earlier points, and in the limiting case when the entire surviving stock is removed simultaneously production will reach its maximum value at the cropping point. Assuming that the relation between the stock and production before cropping point remains unchanged, it is evident that in the limiting case the optimum point at which to crop is that at which the stock forms the maximum proportion of the production to date. This proportion has been plotted in Figs. 15 and 16 and is shown to be at its maximum slightly before the maximum level of the stock is reached; that is, about the beginning of the second year in the lower waters, and about the middle of the second year in the upper waters. Thus, under these conditions the optimum cropping point becomes earlier as the intensity of cropping increases. This is the reverse effect to that shown by Ricker to be necessary on the assumption that the production rate is unchanged by intensity of cropping. Since Ricker's assumption will be at least approximately correct when the intensity of cropping is low, while the alternative assumption will be more nearly correct under high cropping intensity, it appears that the optimum point for the commencement of cropping will always occur before the stock reaches its maximum. This will apply unless the total annual production is not limited to a maximum value by food supplies or other causes, but depends solely on the numbers of the population and fixed growth rates.

Since the growth rate in the Horokiwi appears to be dependent on the density of the stock, it would be desirable to fix the point of first cropping rather before the peak of the stock, whatever the intensity of angling. It has so far been assumed that the relation between stock and production before the cropping point is unchanged. Increased intensity of cropping will however reduce the total stock by leaving fewer survivors beyond the cropping point. Where, as in the Horokiwi, a stabilizing mechanism operating through the food supply exists, a reduction in stock will itself increase the rate of production, and this will in turn affect the stock-production relationship and tend to modify the time of optimum cropping. The direction in which this effect will operate may be seen by considering the relation between the food consumption and the surviving stock at successive dates. This has been set out in Table 70, which shows that, except possibly for an early period in the upper waters, the proportion of food consumed which remains

embodied in the stock falls continuously throughout the life of the year-class. Thus, from this aspect, it would appear that the earlier the cropping point the greater is the efficiency with which the food supply is converted into crop. In practice, if the cropping point is brought too far forward the stock may be so reduced that the food consumption falls seriously, causing a decrease in the efficiency of utilization at the first step—the conversion of bottom-fauna production into food ingested. It is evident however that, as long as the total stock is sufficient to utilize the bottom fauna fully, the efficiency with which the bottom fauna is converted into the stock will rise as the cropping point is brought forward. Thus, from this aspect also, the optimum cropping point appears to be in advance of the peak of the stock curve. It is noticeable in Table 70 that in both lower and upper waters the proportion of the food which remains in the stock falls sharply early in the third year; in the lower waters this may be associated with the reduction in the stock by angling, but in the upper waters this does not apply. It would therefore seem to be desirable in both zones to fix the cropping point before this stage in the life of each year-class.

It is thus evident that whatever the nature of the balance between food supply and growth rate, the maximum potential crop will be available in the Horokiwi if cropping begins during, or even slightly before, the second year of life of each year-class, and in the lower waters it should begin somewhat earlier than in the upper waters. We have already seen that in practice cropping begins a full year later in the upper waters than in the lower waters, and it is this difference which is largely responsible for the much reduced efficiency of this stage in the upper waters.

In order to obtain the maximum continuing yield it is necessary however to ensure not only that exploitation is as efficient as possible, but also that an adequate breeding stock is available to start the next generation. If the cropping point is made too early the breeding stock could be imperilled even though the efficiency of cropping was raised. This effect will be further considered in relation to conditions in the Horokiwi at a later stage.

The alternative approach to the problem of improving the efficiency of this step would appear to lie in finding means of reducing the unwanted losses caused by the destruction of trout material already produced. Up to the beginning of cropping about 80 per cent. of the production in the lower waters, and about 93 per cent. in the upper waters, has been lost. These losses are due to the death of the trout by natural causes, including the action of predators, and perhaps to emigration. It would seem that efficiency could be readily improved by reducing this pre-cropping mortality by such methods as the reduction in the number of predators, of which eels may be the most significant. While the efficiency of this step could probably be improved in this way, it is less certain that any corresponding gain in over-all efficiency, and therefore in the actual crop, would result. This is due to the stabilizing mechanism based on the food supply which has already been discussed. The increase in stock which would result initially from a greater survival rate would probably allow less food to be available for production, and this

PLATE XI. The main valley at the peak of the severe flood of 2nd October, 1941. This photograph, which was taken from almost the same point as the frontispiece, shows the extent to which the stream overflowed its banks and spread over the valley floor during this flood.

PLATE XII (a). Part of Zone II M at the peak of the flood of 2nd October, 1941.

PLATE XII (b). The same place a few days after the flood, when the stream had returned to its normal level. The area covered by the flood is now a wide expanse of loose shingle littered with lumps of turf torn from the old stream banks. The electric power pole which was nearest the camera in Plate XII (a) was washed out soon after the photograph was taken, and has been replaced by a new pole farther to the right in this picture.

would in turn tend ultimately to limit the stock to a value nearer the original. Thus the gain in ultimate crop would be less than the decrease in the amount of production going to undesired losses.

The actual extent of the increase in efficiency caused by removal of predators cannot be forecast without very much more comprehensive data than are at present available, and its determination would probably require a series of experiments in which the effects of the removal of predators could be examined. In one of the few such experiments already performed (Ricker and Foerster, 1948), the removal of a large proportion of the predatory fish from Cultus Lake was followed by three seasons in which the total annual production of young sockeye salmon was well above the previous normal. The new level had however been approached in two seasons before the predators were removed, and in those two seasons the sockeye which were exceptionally abundant were also abnormally small at time of migration (Foerster, 1944); it appears likely therefore that in this instance the removal of predators increased the rate of survival and allowed the sockeye population to approach more closely to the production limit than it could normally do before.

The efficiency of the final step in conversion of bottom fauna into angling crop is determined by the proportion of the stock surviving to the cropping point, or produced thereafter, which is taken by anglers. This depends upon the extent and effectiveness of the angling effort. The effectiveness of the effort is determined by such factors as the degree of skill of the anglers frequenting the particular waters, and by the methods and conditions of angling which are legally permitted. In the present case these factors are similar in both lower and upper waters of the Horokiwi, and in fact the average level of skill is probably higher on the upper waters than on the lower. The much greater efficiency of this stage in the lower waters (39 per cent.) than in the upper waters (11 per cent.) is therefore almost certainly due to the greater angling effort in the lower waters (105 hours per mile in 1940–41) than in the upper waters (6 hours per mile in 1940–41). This great difference in angling pressure is probably due to two factors; the much easier nature of the angling in the large and open lower waters compared to the small and frequently overgrown upper waters; and the greater average size and particularly the greater chance of catching relatively large fish, of 2 lb. or more, in the lower waters. It is noticeable that most of the anglers who fish the Horokiwi at all regularly generally concentrate upon either the lower or the upper waters according to the type of angling they find most interesting.

(b) Effect of Regulations

Fisheries management practices in the Horokiwi, as in most New Zealand waters, are limited almost entirely to stocking with fry and to the proclamation and enforcement of a number of restrictive regulations. The significance and probable effect of the liberations has already been discussed, but more detailed consideration may be given to the effects of the regulations. The most important regulations are those which:—

1. Restrict the taking of trout to licensed anglers using one rod and line.
2. Prohibit all baits and lures except artificial fly.
3. Prohibit the taking of more than 12 trout by one angler in one day.
4. Prohibit the taking of fish less than 11 inches in length.
5. Establish a close season between 1st May and 30th September.

The prohibition of the taking of trout except by sportsmanlike methods is presumably intended to ensure that the full available crop of trout can be exploited by the anglers for whose benefit they were introduced and at whose cost the fishery is maintained. From their very nature, it is almost impossible to get reliable data regarding the quantity of fish taken unlawfully, but in an open, well-roaded valley like the Horokiwi it is not likely to be great in normal times. It is generally believed that about 1943, when several large military camps were established in the neighbourhood and ranging was limited by petrol shortage, there was large-scale poaching in the lower Horokiwi, which resulted in serious local depletion of the trout population. We have already seen that from 1942 to about 1947 there was a period of relatively low rates of catch in the Horokiwi; it may be that this was due in part to the poaching referred to, but there is also reason to believe that it was at least partially due to the severe floods of 1941, and it may be significant that a similar period of low rates of catch occurred in the upper waters where there is no rumour of serious poaching.

The restriction of the right of angling to licence holders is probably intended solely to produce revenue to be used for the benefit of the fisheries and not to restrict the number of anglers. That it does in fact have very little restrictive effect is indicated by the evidence that even in times of economic depression there is little or no decrease in the number of licences sold (Hobbs, 1948).

The prohibition of all baits or lures except artificial fly may be made either to ensure the maximum catch for what is felt to be the most sporting method of fishing, or else to try to give a better ultimate return by preventing over-exploitation of the stock by methods which are too effective or too destructive of under-sized fish. As has been pointed out by Hobbs (1948), these restrictions may have the effect of reducing the catch by making it more difficult to take fish at seasons and under conditions which are not suitable for fly-fishing. The prohibited methods, while not necessarily more generally efficient, are suitable for those conditions and thus permit effective angling to be carried out over a greater proportion of the angling season. An essentially biological investigation is not the appropriate place to consider the first of the two possible motives for this restriction, since this is entirely a question of taste. It is however appropriate to consider whether the restriction of the efficiency of angling by limitations on method is likely to achieve the other possible object, an increased ultimate yield. In the lower waters there is an efficiency of only about 39 per cent., and the stock is already decreasing before the fish first become legally takeable. It follows therefore that the more slowly the population is cropped, the greater will be the proportion of the stock which dies from other causes, and therefore the less will be the efficiency of this step in the process of exploitation. Any practice, such as that under discussion,

which reduces the rate of cropping by reducing the effectiveness of angling, will therefore also reduce the efficiency with which the available stock is cropped.

On the other hand, an increase in angling intensity will reduce the number of fish which spawn more than once. Although the bulk of the eggs produced come from the two-year-old fish, the contribution made by the older age-groups is quite significant, and in the lower waters formed about 49 per cent. and 17 per cent. of the total production in the years 1940 and 1941. An increase in angling intensity, brought about by reduced restrictions on method, would therefore tend to cause some, though not a proportionate, decrease in the number of eggs produced in future years. Thus, although the present investigation has not yielded data which enable a definite forecast to be made as to the effect of any relaxation of restrictions on angling method, it has provided some measure of the magnitude of some of the most important factors which have to be taken into account. It is evident that the result would depend on the balance between these conflicting effects, and it is by no means certain that such a change would have any harmful effect upon the yield of trout to the angler.

The fixing of a bag limit, although probably intended to cause a more even distribution of fish among anglers, has actually had the effect of reducing angling intensity, and the same conflicting factors apply as in the case of restrictions on method discussed above. It is however a relatively simple matter to determine whether the bag limit as at present applied produces any significant effect. In the ten seasons studied the limit was only reached in three of the 455 daily bags recorded, and it is obvious therefore that, whatever would be the effect of a smaller bag limit, the limit of twelve now in force has no effect upon the stock of fish or upon anglers' catches.

The size-limit is the most important of the restrictive regulations in its effect upon the trout population, and upon the crop of fish, because it determines the point at which a year-class is first cropped. Throughout the period of this study the legal limit was 11 inches total length; this corresponds approximately to a fork length of 27.9 cm. Table 38 shows that in the 1939 year-class a fish of mean length reached this size in about November, 1940 and March, 1941 in the two zones of the lower waters. In the upper waters this size had not been attained by the 1939 year-class by the time the investigation ended in October, 1941, but Tables 40 and 41 show that the older year-classes reached 11 inches in about August of the second year in Zone III, in October of the third year in Zone V, but not until the fourth year in Zone IV. It has been shown earlier that to make cropping as efficient as possible it should begin during the second year of each year-class, preferably towards the beginning of the year in the lower waters, and towards the end of the year in the upper waters. Table 38 shows that at the end of its second angling season, i.e., 30th April, 1940, the mean length of the 1939 year-class was 32.1 cm. and 27.5 cm. in Zones I and II respectively. If the relative deviation is 0.075, which is the normal value at this age, then about 3 per cent. of the Zone I fish and 50 per cent. of the Zone II fish were still below the size-limit at the end of the season. In the combined population of the lower waters,

about 25 per cent. would be under-sized at the end of their second season. In the same way it can be shown that on 1st January, which is a convenient central date for the distribution of angling pressure, about 58 per cent. would be under-sized. The effect of the size-limit is therefore to restrict severely the extent to which a year-class in its second year can be cropped in the lower waters. This effect has also been shown by the relatively small numbers of second-year fish in the angling catch as distributed in Table 55. By the beginning of the third season, on the other hand, less than 2 per cent. of the population of the lower waters is below the limit, and in this season the fish are therefore completely available for cropping. It would appear from this that in the lower waters cropping begins rather too late to give maximum efficiency of utilization.

The effect of the size-limit on the survival of adequate spawning stock must however also be considered. In the Horokiwi no trout spawn in their first winter, but the great majority spawn in their second winter. Excessive cropping during the second summer would therefore tend to reduce seriously the egg production in the following spawning season. The limited amount of cropping allowed by the 11-inch size-limit does not have any great effect in this way; in 1940 and 1941 the egg production by second-year fish in the lower waters would only have been increased by about 17 per cent. and 8 per cent. respectively if all the fish of this age-group which were caught by anglers had not only escaped the anglers but had also survived all other perils and spawned successfully. The effect of the 11-inch limit in the lower waters is therefore to allow a limited amount of cropping in the second summer, when it is desirable for maximum efficiency, but to ensure that the majority of fish are protected until they have spawned in their second winter, and then to allow them to be fully available to anglers. This size-limit appears therefore to be fixed at almost exactly the point which is most desirable on biological grounds.

A different situation exists in the upper waters. Here the average fish does not reach the size-limit until the third summer even in the zones where growth is most rapid, and as a result the fish do not become fully available to anglers until the fourth year. This is illustrated by Table 61 which shows that in 1940–41 only 0.3 per cent. of the mortality among third-year fish was due to angling, while in the fourth-year fish it had risen to 8.8 per cent. It is clear therefore that effective cropping does not begin for a year and a half after the time necessary to give maximum efficiency of utilization, and it is also delayed a year longer than is necessary to ensure an adequate breeding stock. The reduction in breeding stock, which an earlier cropping date could produce, might indeed increase the efficiency of conversion of bottom fauna to trout, which, apparently as a result of the denser stock, is less than in the lower waters. More efficient conversion could be achieved by fixing a size-limit which was reached by the average fish during its second winter. No great accuracy is possible on account of the divergence in growth rates between Zone IV and Zones III and V, but a limit of about 24 cm., or 9½ inches, would probably be more effective.

There are of course difficulties of enforcement if different size-limits are imposed on different sections of one small stream, and, if uniformity is essential, it is

probably desirable to give the greater weight to conditions in the more popular water. There seems no doubt, however, that in the Horokiwi the angling crop could be increased by the institution of different size-limits on the lower and upper waters.

A close season during the time the trout were spawning was probably originally instituted with the idea that at this time, when their eggs are ripe, they are more valuable to the future of the race than they are earlier. It is becoming more generally realized however that this belief is largely fallacious, and that there is little difference in the reproductive potential of a fish at the spawning season or a few months earlier. In the lower waters of the Horokiwi, however, it appears that conditions are such that the close season may be unusually effective in assuring the size of the surviving breeding-stock. The majority of eggs are produced by the fish in their second year, and during the open season these fish are largely protected by the size-limit; this protection is however rapidly removed as the fish grow, and by the end of the season about 75 per cent. are legally takeable. If angling were continued up to and during the spawning season, nearly all the second-year fish would become takeable, and they would probably form the greater part of the angling catch. Thus, if angling were allowed throughout the year, and if anglers availed themselves of the opportunity, there might be a tendency towards depletion of the stock of two-year-old fish before they had spawned. Lengthening of the angling season would also tend to increase the general intensity of angling, but the effects of this cannot at present be foretold, and there might be a tendency for individual anglers to spread the same amount of angling time more thinly over the longer season.

(c) Numerical Efficiency

The efficiency of the various stages in the production cycle which leads up to the trout crop has so far been considered only in terms of weight, but the numerical aspects of the problem may also be briefly examined. The following table summarizes these aspects of the results:—

	Lower Waters	Upper Waters
Eggs produced	100%	100%
Surviving when cropping begins	0.15%	0.052%
Angling crop	0.075%	0.004%

Efficiency is bound to be very much less on a numerical basis than on a weight basis since we start with newly-hatched fry weighing about 0.1 gm. each and take a crop of fish averaging about 400 gm. If numbers of fish were the only consideration, efficiency could be increased by bringing the cropping point forward by lowering or even removing the size-limit, and it is apparently this reason that has led Needham, Moffett and Slater (1945) to suggest the desirability of removing size-limits under certain environmental conditions. Anglers generally however are interested not only in the numbers but also in the size of the fish they catch, and many prefer a limited number of good-sized fish to larger numbers of small ones. It is probable that the criterion of maximum total weight of catch, which

represents optimum efficiency from the biological standpoint, is also that which is generally most acceptable to anglers. An earlier cropping point which gave greater numerical efficiency would of course also remove a higher proportion of fish before they had spawned, and might therefore have a depleting effect on the population.

7. THE EFFECT OF FLOODS

In the preceding sections the structure and relationships of the Horokiwi trout population have been analysed in considerable detail. This analysis has been based on events during the year May, 1940 to May, 1941 when fairly normal conditions were assumed to exist. The term "normal" is here intended to describe the conditions which occurred during a time when the stream was in a fairly stable state, following about three years without heavy flooding, and when there was little serious disturbance during the period of observations. That a completely stable state had not been established during the few years preceding the observations is indicated by the irregularities which were found to exist in the relative strengths of the different year-classes, particularly in the upper waters. Conditions during the "normal" period were also affected by the severe flood of February, 1941 which caused extensive disturbance of the river bed, destruction of a proportion of the bottom fauna, and a reduction in the growth rate of the trout. It is unfortunate that it is necessary to include the period between this flood and May, 1941 in order to obtain data for a year which was even approximately normal. Conditions were however fairly dry between the end of February and May, and there was some degree of recovery of the stream bed and the bottom fauna.

Between May and the time when the last observations were made in October, 1941, very wet weather prevailed and there were numerous floods and freshes of varying magnitude, which caused very extensive damage to the stream bed, the fauna, and the trout population. Comparison of conditions in this period and in the corresponding period in 1940 enables an estimate to be made of the effect of these floods on the production of trout.

Before considering the effect of the floods on production, the measured effects on the basic quantities involved may be briefly recapitulated.

The bottom fauna is estimated to have been reduced during most of 1941 to about 40–50 per cent. of the 1940 values, although there may have been a temporary recovery about May and June. In Zone II, which consistently showed the heaviest damage, it may even have been reduced to 20–25 per cent. of the 1940 values.

In most year-classes the estimated number of fish present in October, 1941 was about a quarter to a half of that of fish of the same age in October, 1940.

About 80–90 per cent. of the ova produced in 1941 were probably destroyed by floods, as against a negligible amount in the previous year.

In Zone II, where the flood effects were most severe, the mean individual weight of the 1940 year-class in May, 1941 was only 77 per cent. of that of the 1939 year-class at the same time in the previous year, and smaller reductions occurred

in other zones. This difference was maintained up to October, 1941. The older year-classes also showed a reduction in size compared with fish of similar age in the previous year.

The condition factor of the 1939 year-class in Zone II was, in May, 1941, as much as 5 per cent. below that of corresponding fish in the previous year.

The reductions in rate of growth and in the number of fish both contribute towards a reduction in stock and in production in 1941 as compared with 1940. The data regarding the production and food supply relationship are summarized in Table 71. Owing to the limited nature of the observations the results have been grouped into lower and upper waters in order to smooth out some of the random irregularities. The table shows that in October, 1941 the stock in the lower and upper waters was 154 kg. and 117 kg. respectively, as against 777 kg. and 417 kg. in 1940; the stock had therefore been reduced to 20 per cent. and 28 per cent. of the previous year's values. Similarly production between May and October, 1941 was 115 kg. and 61 kg., compared with 555 kg. and 143 kg. in 1940; in this case the reduction is to 21 per cent. and 43 per cent.

Table 71. Data regarding trout production during the flood period May–October, 1941, for comparison with the events of a normal year.

	Lower Waters.	Upper Waters.
Stock in October, 1941	154 kg.	117 kg.
Production, May–October, 1941 ..	115 kg.	61 kg.
Maintenance food requirement ..	869 kg.	387 kg.
Production food requirement ..	483 kg.	255 kg.
Percentage of food used for production	35·8	39·7
Ratio of maintenance food to mean bottom fauna	12·8	22·9

The reduction in both stock and production in 1941 involved a reduction in the food consumption of the trout. There was, however, also a decrease in the density of the bottom fauna from which this food was obtained. Table 71 shows the estimated food requirements for maintenance and growth during the period May to October, 1941, in both lower and upper waters, the data being summarized from Table 64. The percentage of food used for production is obviously much less than the normal values for 1940, when, for the corresponding period, the percentages used for production were 64 per cent. and 46 per cent. in the lower and upper waters respectively. The reduction in the proportion of food used for maintenance appears to have been less in the upper waters which were also less affected by the floods.

Under normal conditions, the proportion of food which is used for production tends to be correlated with the extent of the demands made by the trout upon the bottom fauna. These demands have been measured as the ratio between the estimated annual food consumption for maintenance purposes and the average density of the bottom fauna. It varied between 11.8 in Zone II R and 63.8 in

Zone IV. Table 71 shows that this ratio for the period May to October, 1941 was 12.8 in the lower waters and 22.9 in the upper waters; if scaled up to a full year's food consumption at this rate, the ratios are 30.6 and 54.7. An alternative comparison may be made by determining the corresponding ratios for the period May to October, 1940; these are found to be 7.3 and 16.8 respectively. The effective reduction of the fauna, and therefore the increase in the pressure upon it, was probably greater than these figures suggest, since, as is shown by Table 22, the numbers of two of the most important food-animals, *Deleatidium* and *Pycnocentrodes,* were particularly heavily reduced by the floods.

Thus, in 1941 the reduction in the bottom fauna appears to have been sufficient to increase the proportion of it which was used by the trout for maintenance purposes, despite the reduction in the trout stock. This increased pressure on the food supply probably caused the reduction in the proportion of the food intake which was used for growth and production. Thus the floods in 1941 produced an extension of the process whereby under normal conditions the food supply tends to stabilize the stock by limiting production of trout. They caused a reduction in the bottom fauna which limited the stock of trout to a new and lower level. This occurred independently of the numerical reduction brought about by the floods. The limitation was presumably only temporary, and, as the stream bed became stable again under the drier conditions of subsequent years, the bottom fauna was able to increase in density and so allowed the trout stock to rise, until equilibrium was again attained, possibly at or near the original level. It is unfortunate that the enforced cessation of this study in October, 1941 prevented any attempt to follow the recovery process.

This investigation leads therefore to the conclusion that:—

(a) In the Horokiwi there occurs a population of trout in which the annual production is largely limited by the food supply;

(b) Under present regulations and angling intensities the fishing pressure is not significantly affecting the trout production.

The food supply, derived mainly from the bottom fauna, may in turn tend to be held at a steady level under stable stream conditions by its own supplies of food, but it is also limited from time to time by the destructive action of floods, which cause an abrupt reduction in the stock of the bottom fauna, from which there is only a gradual recovery. These changes bring about parallel movements in the production, and therefore in the stock, of trout. While, therefore, under continuously stable conditions, both the bottom fauna and the trout stock would also be stable, there are periods of variable occurrence and duration in which both bottom fauna and trout production are limited, directly and indirectly, by the action of floods. It is believed that during 1940 a condition of stability was approached, in which production at both levels was probably being controlled by other factors, but that throughout most of 1941 production was being limited by the effect of the floods which occurred in that year. These effects were probably increased in some parts of the stream by efforts to control and repair flood damage by channel construction and straightening.

8. SUMMARY

The detailed information regarding the trout population and the bottom fauna has been used to provide estimates of the quantities of material flowing along the various paths in a section of the food-chain centred on the trout, and having the structure shown in Fig. 14.

Discussion is centred on three key quantities, the *stock*, the *production*, and the *crop*.

The *stock* is the amount of material embodied in the trout at any one time. The stock of each year-class in each zone is shown for a number of dates in Table 58. The density of the total stock appears normally to be fairly constant, and varies for different zones between 100 and 400 lb./acre. The total stock of the stream was normally about 1100 kg. The stock was greatly reduced in 1941 as a result of the effects of the floods on both the rate of growth and the numbers of the trout. The stock of any year-class builds up rapidly to a maximum in the second summer and then declines again more slowly. The peak is rather later and more prolonged in the upper waters than in the lower.

The *production*, which is the amount of material becoming embodied in the trout during a given period, was estimated for each year-class in each zone by measuring the area enclosed under a graph of number of survivors against mean individual weight, and the results are shown in Table 59. The density of production in a normal year varies between 250 and 750 lb./acre in the different zones, and the total annual production is about 2278 kg. Production in 1941 was much reduced by the action of floods, and in May–October, 1941 was only about one-quarter of that in May–October, 1940. About 95 per cent. of the total production of a year-class has been accomplished by the end of the second year. The percentage of the production to date which is surviving as the stock of a year-class falls rapidly at first and then rises again to a maximum of 30–35 per cent. about the end of the first year; by the end of the second year it has fallen to 12–20 per cent.

The *crop* is the part of the production taken by anglers. In the lower waters cropping begins in the second year and all fish are takeable in their third year; in the upper waters it does not begin until the third year, and most fish are not takeable until their fourth year. The proportion of the ultimate production which has been removed by natural causes before a year-class becomes fully available for cropping is 80 per cent. in the lower waters, and 93 per cent. in the upper waters; after it begins, cropping accounts for 27 per cent. and 13 per cent. respectively of the remaining part of the production. The relation between production, stock, and crop is shown graphically in Figs. 18 and 19.

Food requirements were estimated from the results of experiments by other workers; the maintenance requirement was taken to be 1.23 per cent. per day, and the efficiency of conversion of food used for growth as 23.8 per cent. The relation between food consumption and the other quantities studied is shown in Fig. 22. The crop is only equal to 1.04 per cent. and 0.13 per cent. of the total food consumed by trout in the lower and upper waters respectively. Comparison between the zones suggests that the food supply tends to limit the production of trout,

since as the pressure on the food supply increases the actual density of the bottom fauna decreases, and the proportion of the food drawn from it which can be used for growth also decreases. The amount of bottom fauna consumed in a year by trout is between 40 and 150 times the amount present at one time in different zones. The daily food consumption is 7 to 16 times the average stomach contents but varies with the temperature.

Except, perhaps, for the close season, the only management practice which has any significant effect on the crop of trout at present is the size-limit. This determines the time of cropping in a year-class; in the lower waters the 11-inch limit gives a very satisfactory balance between the cropping point desirable for maximum efficiency and that necessary to protect the breeding stock; in the upper waters the cropping point is much too late, and leads to very inefficient utilization. A $9\frac{1}{2}$-inch limit is probably the optimum.

The floods of 1941 caused some reduction in the numbers of trout but the balance between trout stock and food supply caused the growth rate of trout to decrease as a result of the destruction of the bottom fauna. It is probable that, while the bottom fauna and hence trout production may be limited by its food supply in times of continuous stability, the sudden decreases and slow recoveries caused by floods may also be an important controlling factor.

PART VI

Conclusion

It has been stated in the introduction that the investigation described in this report was intended primarily as an experiment in technique. The object was to determine how extensive a quantitative study of the fundamental factors affecting the productivity of a trout population could be made with the very limited resources available. In assessing the results of the experiment, consideration must be given to the completeness with which the inter-related phenomena were observed, and to the accuracy of the results obtained.

As much information as was practicable regarding the basic physical and biological features of the environment inhabited by the trout population studied has been included in this report, but quantitative observations have been restricted to those directly relating to the trout population and its food supply. The physical survey of the environment, including measurement of the dimensions, was necessary to enable quantitative data collected by completely different sampling procedures to be collated, and to enable adjustments to be made for the variety of environments found within the single stream. The only quantities within the scope of the inquiry which were susceptible to direct measurement were the stocks of bottom fauna, native fish and trout, and the crop taken by anglers. All of these, except the stock of native fish, were the subjects of major sections of the inquiry, and were measured to a degree of accuracy which has been estimated. Information regarding the stock of native fish was only obtained incidentally and is little more than qualitative. While they form an important part of the biological community inhabiting the Horokiwi, it is unlikely that any native fish, except eels, are of any great importance to the production of trout. The production of trout and their food requirements have both been computed by fairly simple methods from the basic data. Production can only be determined in this indirect way and there seem to be no means available for an independent check. Food consumption, on the other hand, could be measured more directly by methods similar to those used by Borutzky (1939a) if sufficient resources were available.

An important aspect of the dynamics of the trout population is concerned with the fate of that part of the amount produced which does not enter the crop. Even in the most heavily fished parts of the stream this is much the larger part of the production, and no direct evidence as to its fate has been obtained. It may be assumed that a significant proportion is taken by predators, of which the eel is probably the most important, and deaths of old fish, apparently as a sequel to spawning, have been observed on a few occasions. No evidence was obtained as to other causes of death or as to the proportions removed from the stock in various ways. It would appear that the quantitative study of this section of the problem would form a very valuable addition to an investigation of this type. In addition to assisting in the understanding of the relationship between the trout and other members of the community, such data, if sufficiently quantitative, would provide a valuable check on the other measurements.

Increased accuracy in the computation of food consumption by the methods used in this study would require, in addition to improved estimates of stock and production, more comprehensive information regarding the food requirements of trout under various conditions of age and environment. This would be necessarily an experimental study, but there are certain difficulties in simulating in the laboratory the essential features of the natural environment. As an example, it seems not unlikely that the food required for maintenance by a wild fish, which has to move about seeking its food and to maintain its position against the stream, may differ significantly from that of a hand-fed fish in the comparatively still water of a tank or laboratory trough. The estimation of food consumption could also be attempted by making more use than is so far possible of data regarding the amounts of food present in the stomachs of the wild fish under various conditions. This again would require an experimental approach, and it would be necessary to examine the effect of such factors as rate of feeding, temperature, nature of food and age of trout.

The present study has suggested that a significant relationship exists between the food supply, as represented by the bottom fauna, and the production of trout. A better understanding of this relationship requires a more detailed knowledge of the dynamics of the bottom fauna, and, particularly, of its production. The data so far available concerning the bottom fauna have yielded only estimates of the stock and of the crop taken by the fish. The study of the trout population has emphasized that, for any population, the stock and crop are both ultimately dependent on the amount produced, and that any attempt to compare them with each other or with other quantities can have only limited value unless the production is also known. The Horokiwi data have indicated the existence of an unexpectedly high ratio between the annual crop of bottom fauna taken by trout and the average stock of bottom fauna, but this result cannot be satisfactorily verified or explained without additional basic data on the production of bottom fauna.

The data obtained in this study have been sufficiently comprehensive to give a quantitative account of the flow of matter through the trout population of this, apparently typical, stream and to give a measure of the relation between the amounts which take the various paths. Analysis of the results has also indicated sections of the field in which further development of the work would be most profitable, either to provide more detailed knowledge of parts of the system already examined in outline, or to obtain information concerning related parts of the system which would assist in the interpretation of the knowledge already gained.

During this study considerable attention has been paid to the determination of the probable degree of accuracy of the various estimates. The approximate limits for 95 per cent. confidence may be briefly summarized:

Area of stream bed	± 5%
Density of bottom fauna	± 50% (higher for particular forms)
Numbers of adult trout	± 50% at best
Weight of trout	± 5%
Weight of stomach contents	± 22%
Crop	+0 to −10%

It is evident that the two quantities with the largest possibility of error are unfortunately the most basic, i.e., the densities of the bottom fauna and of the trout population. The general level of accuracy with which most of the relationships have been estimated may therefore be taken to be about ± 50 per cent. While this may seem to be a very low degree of accuracy, it is believed that estimates obtained in a theoretically satisfactory manner to a known, though low, degree of accuracy provide a much more useful basis for the study of the dynamics of a population than do those based on untested and sometimes unsound hypotheses, such as the assumption that production and crop are identical. This view has also been put forward by Ricker and Foerster (1948) in the following words:

"Thus if a computation of production differs from the true value even by 50 per cent., it is still a much better piece of information than is the yield for the purpose of estimating the utilization of fish food resources, or in connection with most other questions involving the 'trophic-dynamic' aspect of aquatic ecology."

Improvement in the over-all accuracy of the results can come most quickly from identification of those sections of the investigation in which the level of accuracy is lowest, and from the subsequent development of methods of increased accuracy, or by the devising of independent checks for these sections. It would for instance be valueless to try to improve upon the results of the present study by finding means of increasing the accuracy of the estimates of the average weight of the fish. It is obvious that in the present instance the accuracy of the whole study is limited by the accuracy of the estimates of the density of the trout and bottom fauna populations, and any similar study which was aimed at obtaining results of a higher degree of accuracy would, of necessity, call for methods yielding more reliable estimates of these quantities. It seems at present that the major difficulty in the estimation of the bottom fauna lies in the handling of adequate numbers of small unit area samples on which this estimate is usually based, and the solution probably lies in the development of improved methods for the mechanized handling and sorting of the material in the laboratory. The cage method of Ide (1940) may also be of value, particularly if the production of bottom fauna is to be studied, although the difficulty of obtaining an adequate number of samples appears to be even greater than in the bottom sampling methods. Improvement in the accuracy of the estimates of the trout population seems to require chiefly more rapid and, particularly, more efficient means of catching random samples of fish. Such methods would increase the numbers of fish actually captured, and would thus automatically reduce the relative size of the sampling errors in the subsequent estimates. They would, incidentally, provide increased quantities of material for the estimation of size and growth rate, although, in view of the relatively high degree of accuracy already obtainable for these quantities, it would perhaps be no longer necessary to use all the available material for this purpose, except in the less numerous classes of fish such as the older age-groups.

In conclusion, it is believed that the investigation which has been described has yielded information regarding the structure and dynamics of a trout population which, despite its relatively low level of accuracy, will assist in the understanding of the fundamental factors controlling the production and cropping of fish populations, and has also indicated ways in which studies of a similar nature may be improved.

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APPENI

Summarized results of the faunistic collections; showing for ea
the mean number in the collections taken in that month, the esti ma
percentage in the estimated mean fauna. Re

ZONE

	Dec., 1939–Jan., 1940. Mean No.	Est. No.	Est. %	April, 1940. Mean No.	Est. No.	Est. %	June, 1940. Mean No.	Est. No.	Est. %	August, 1940. Mean No.	Est. No.	Es %
Hydropsyche	21·7	10·4	*1·8*	7·6	9·9	*1·6*	5·7	5·4	*2·1*	4·0	4·4	*0*
Rhyacophilidæ larvæ	4·0	2·2	*0·4*	1·0	1·2	*0·2*	0·7	1·9	*0·7*	2·0	3·1	*0*
„ pupæ	0·0	0·0	*0·0*	0·9	0·9	*0·1*	0·0	0·7	*0·3*	2·7	2·6	*0*
Helicopsyche	3·0	4·5	*0·8*	19·9	4·6	*0·8*	7·7	7·6	*2·9*	5·7	8·3	*1*
Olinga larvæ	1·5	0·9	*0·2*	0·7	2·8	*0·5*	1·0	2·9	*1·1*	0·5	5·5	*1*
Sericostomatidæ—												
* Type "C" larvæ	0·2	2·2	*0·4*	1·7	1·5	*0·2*	1·5	2·5	*1·0*	1·5	1·7	*0*
„ pupæ	0·2	0·1	*0·0*	0·1	0·1	*0·0*	0·0	0·0	*0·0*	0·2	0·3	*0*
Pycnocentrodes larvæ	80·0	40·8	*7·2*	27·9	18·9	*3·1*	6·0	28·8	*11·1*	40·2	34·0	*7*
„ pupæ	3·5	2·0	*0·4*	9·6	4·9	*0·8*	0·0	0·0	*0·0*	0·0	0·0	*0*
Coloburiscus	0·2	1·2	*0·2*	1·7	3·3	*0·5*	3·5	2·5	*0·9*	1·0	1·5	*0*
Deleatidium	47·7	30·4	*5·3*	91·1	94·6	*15·5*	52·0	68·2	*26·4*	55·2	83·5	*17*
Leptoperlidæ	0·0	0·1	*0·0*	0·5	0·4	*0·1*	0·5	0·3	*0·1*	0·0	0·4	*0*
Parnidæ imagines	5·5	4·5	*0·8*	0·2	0·9	*0·1*	0·0	0·4	*0·2*	0·0	0·4	*0*
„ larvæ	437·2	420·5	*73·8*	343·2	330·0	*54·0*	18·0	40·3	*15·6*	198·2	40·3	*8*
Chironomidæ larvæ	0·5	1·4	*0·2*	9·2	23·2	*3·8*	10·0	35·3	*13·6*	248·0	161·7	*33*
„ pupæ	0·0	0·0	*0·0*	0·4	12·3	*2·0*	0·2	4·1	*1·6*	42·0	27·9	*5*
Simuliidæ larvæ	0·2	0·2	*0·0*	0·2	0·4	*0·1*	3·5	2·4	*0·9*	0·2	2·4	*0*
„ pupæ	0·0	0·3	*0·1*	0·0	0·0	*0·0*	0·2	0·2	*0·1*	0·5	0·2	*0*
Other Diptera larvæ	0·7	0·9	*0·2*	1·9	0·9	*0·1*	1·5	1·1	*0·4*	6·5	3·0	*0*
Potamopyrgus	56·5	42·8	*7·5*	193·7	157·0	*25·7*	42·0	47·8	*18·5*	113·0	85·3	*17*
Latia	0·0	0·1	*0·0*	0·0	0·3	*0·0*	0·0	0·5	*0·2*	0·2	0·2	*0*
Oligochaeta	2·5	3·8	*0·7*	3·1	4·0	*0·7*	1·5	5·9	*2·3*	11·2	11·7	*2*
Total	665·1	569·3	*100·0*	714·6	672·1	*99·9*	155·5	258·8	*100·0*	732·8	478·4	*99*

ZONE

	Dec., 1939–Jan., 1940. Mean No.	Est. No.	Est. %	April, 1940. Mean No.	Est. No.	Est. %	June, 1940. Mean No.	Est. No.	Est. %	August, 1940. Mean No.	Est. No.	Es %
Hydropsyche	..	8·6	*3·7*	..	8·1	*2·3*	4·2	4·4	*1·6*	3·5	3·6	*0*
Rhyacophilidæ larvæ	..	4·0	*1·7*	..	2·1	*0·6*	3·3	3·3	*1·2*	5·1	5·3	*0*
„ pupae	..	0·0	*0·0*	..	1·6	*0·5*	0·8	1·2	*0·4*	2·8	4·5	*0*
Helicopsyche	..	41·1	*17·5*	..	43·6	*12·3*	116·4	70·6	*25·0*	96·7	76·6	*11*
Olinga larvæ	..	1·6	*0·7*	..	4·9	*1·4*	9·5	5·1	*1·8*	9·6	9·7	*1*
Sericostomatidæ—												
Type "C" larvæ	..	37·7	*16·0*	..	24·7	*7·0*	30·6	42·2	*14·9*	16·0	29·0	*4*
„ pupæ	..	1·3	*0·6*	..	0·4	*0·1*	0·0	0·1	*0·0*	1·9	3·4	*0*
Pycnocentrodes larvæ	..	38·5	*16·4*	..	17·8	*5·0*	17·9	27·2	*9·6*	41·4	32·1	*4*
„ pupæ	..	1·7	*0·7*	..	4·4	*1·2*	0·0	0·0	*0·0*	0·0	0·0	*0*
Coloburiscus	..	4·1	*1·7*	..	11·3	*3·2*	3·2	4·1	*1·5*	1·5	2·7	*0*
Deleatidium	..	21·2	*9·0*	..	66·1	*18·7*	43·5	47·7	*16·9*	69·3	58·5	*9*
Leptoperlidæ	..	0·2	*0·1*	..	0·6	*0·2*	0·2	0·4	*0·1*	0·3	0·8	*0*
Parnidæ imagines	..	0·8	*0·3*	..	0·1	*0·0*	0·2	0·1	*0·0*	0·3	0·1	*0*
„ larvæ	..	63·2	*26·9*	..	49·5	*14·0*	17·6	6·1	*2·2*	25·5	6·1	*0*
Chironomidæ larvæ	..	4·3	*1·8*	..	69·5	*19·7*	77·6	46·8	*16·6*	258·5	327·3	*50*
„ pupæ	..	0·0	*0·0*	..	30·3	*8·6*	11·7	10·7	*3·8*	57·7	68·5	*10*
Simuliidæ larvæ	..	0·5	*0·2*	..	0·8	*0·2*	3·9	5·4	*1·9*	6·1	5·3	*0*
„ pupæ	..	0·8	*0·3*	..	0·0	*0·0*	0·2	0·3	*0·1*	0·1	0·3	*0*
Other Diptera larvæ	..	0·7	*0·3*	..	0·7	*0·2*	1·1	0·9	*0·3*	2·9	2·5	*0*
Potamopyrgus	..	4·6	*2·0*	..	16·3	*4·6*	16·6	5·1	*1·8*	15·6	9·1	*1*
Latia	..	0·0	*0·0*	..	0·1	*0·0*	0·2	0·1	*0·0*	0·0	0·1	*0*
Oligochaeta	..	0·6	*0·3*	..	0·6	*0·2*	2·5	0·9	*0·3*	1·4	1·7	*0*
Total	..	235·5	*100·2*	..	353·5	*100·0*	361·2	282·7	*100·0*	616·2	647·2	*99*

*This form has since been identified as an additional species of *Pycnocentrodes*, distinct from *P. chil*

)IX I

ch month in which collections were made and for each form, ıted mean number per square foot for the whole zone, and the ·sults for each zone tabulated separately.

I

t.	October, 1940. Mean No.	Est. No.	Est. %	December, 1940. Mean No.	Est. No.	Est. %	February, 1941. Mean No.	Est. No.	Est. %	April, 1941. Mean No.	Est. No.	Est. %	October, 1941. Mean No.	Est. No.	Est. %
·9	2·5	4·6	*1·1*	10·5	6·7	*1·5*	4·7	6·9	*6·0*	11·5	8·2	*2·7*	2·8	2·6	*3·6*
·6	1·2	2·1	*0·5*	5·7	3·1	*0·7*	0·2	1·2	*1·0*	2·5	1·7	*0·6*	0·4	0·4	*0·5*
·5	2·2	2·4	*0·6*	2·5	2·0	*0·4*	0·2	0·4	*0·3*	1·2	1·0	*0·3*	0·4	0·4	*0·5*
·7	9·2	7·9	*1·9*	7·7	4·4	*1·0*	2·2	2·3	*2·0*	5·5	4·8	*1·6*	7·8	7·2	*9·8*
·1	0·5	3·7	*0·9*	11·0	3·0	*0·7*	0·2	0·9	*0·8*	1·7	1·3	*0·4*	0·5	0·6	*0·8*
·4	1·7	1·1	*0·3*	0·7	0·8	*0·2*	0·0	0·2	*0·2*	0·5	0·3	*0·1*	5·2	5·9	*8·0*
·1	1·0	1·1	*0·3*	0·7	0·5	*0·1*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*
·1	54·0	37·5	*9·2*	40·0	30·9	*6·8*	3·7	2·8	*2·4*	13·2	13·0	*4·2*	4·5	4·2	*5·7*
·0	0·5	2·0	*0·5*	8·7	3·0	*0·7*	0·2	0·2	*0·2*	0·2	0·1	*0·0*	0·0	0·0	*0·0*
·3	1·7	1·2	*0·3*	1·0	1·7	*0·4*	0·0	1·1	*1·0*	17·7	16·1	*5·2*	4·4	4·3	*5·9*
·5	70·7	67·3	*16·4*	98·0	75·1	*16·6*	18·0	25·5	*22·1*	93·2	93·2	*30·2*	19·3	20·6	*28·0*
·1	0·2	0·1	*0·0*	0·2	0·4	*0·1*	0·2	0·4	*0·3*	1·5	1·6	*0·5*	0·0	0·0	*0·0*
·1	0·0	0·4	*0·1*	5·7	4·5	*1·0*	0·2	0·2	*0·2*	0·2	0·2	*0·1*	0·0	0·0	*0·0*
·4	141·0	140·0	*34·2*	112·5	165·7	*36·6*	43·7	53·9	*46·7*	94·0	98·8	*32·0*	18·2	20·2	*27·5*
·8	10·2	50·3	*12·3*	38·7	92·7	*20·5*	4·2	4·7	*4·1*	23·5	26·4	*8·6*	0·0	0·0	*0·0*
·8	0·5	9·4	*2·3*	2·5	9·1	*2·0*	0·0	0·0	*0·0*	1·0	1·1	*0·4*	0·0	0·0	*0·0*
·5	6·5	2·9	*0·7*	0·7	1·0	*0·2*	0·2	0·1	*0·1*	1·0	0·9	*0·3*	0·0	0·0	*0·0*
·0	2·2	1·1	*0·3*	0·5	2·0	*0·4*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*
·6	3·7	4·0	*1·0*	0·5	4·5	*1·0*	1·2	1·2	*1·0*	2·5	2·5	*0·8*	0·0	0·0	*0·0*
·9	33·7	60·6	*14·8*	47·5	35·8	*7·9*	10·7	12·4	*10·8*	36·7	33·6	*10·8*	2·5	6·2	*8·4*
·0	0·5	0·1	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·2	0·2	*0·1*	0·0	0·0	*0·0*
·4	11·2	9·7	*2·4*	5·0	4·9	*1·1*	0·0	1·0	*0·9*	4·0	3·5	*1·1*	0·8	0·9	*1·2*
·8	354·9	409·5	*100·1*	400·3	451·8	*99·9*	89·8	115·4	*100·1*	311·8	308·5	*100·0*	66·8	73·5	*99·8*

II

t.	October, 1940. Mean No.	Est. No.	Est. %	December, 1940. Mean No.	Est. No.	Est. %	February, 1941. Mean No.	Est. No.	Est. %	April, 1941. Mean No.	Est. No.	Est. %	October, 1941. Mean No.	Est. No.	Est. %
·6	1·9	3·8	*1·0*	5·9	5·5	*1·3*	2·1	2·5	*4·1*	2·7	2·9	*1·8*	0·0	0·3	*0·7*
·8	2·1	3·8	*1·0*	6·7	5·4	*1·3*	0·1	0·2	*0·3*	0·3	0·2	*0·1*	0·4	0·4	*0·9*
·7	3·7	4·2	*1·1*	3·0	3·4	*0·8*	0·3	0·4	*0·7*	0·7	0·9	*0·5*	0·0	0·1	*0·2*
·8	74·8	73·4	*19·7*	49·7	40·9	*9·8*	8·0	7·3	*12·1*	20·2	15·2	*9·5*	15·6	8·3	*19·0*
·5	6·4	6·4	*1·7*	4·9	5·5	*1·3*	1·4	9·9	*16·4*	1·3	1·4	*0·9*	0·0	0·3	*0·7*
·5	10·2	19·2	*5·2*	6·0	14·3	*3·4*	13·5	12·7	*21·0*	10·2	26·9	*16·8*	6·5	11·0	*25·2*
·6	7·7	10·7	*2·9*	3·2	4·6	*1·1*	0·3	1·6	*2·6*	1·6	1·2	*0·7*	0·0	0·0	*0·0*
·9	33·0	35·4	*9·5*	34·4	29·1	*7·0*	1·5	2·7	*4·5*	14·3	12·7	*7·9*	4·5	3·6	*8·3*
·0	3·4	1·7	*0·5*	2·6	2·7	*0·6*	0·0	0·0	*0·0*	0·1	0·1	*0·1*	0·0	0·0	*0·0*
·4	0·6	2·0	*0·5*	2·7	2·7	*0·6*	0·4	0·3	*0·5*	2·3	3·5	*2·2*	1·6	1·5	*3·4*
·0	35·2	47·1	*12·6*	63·3	52·6	*12·7*	10·3	9·1	*15·0*	33·1	33·2	*20·7*	12·9	9·8	*21·3*
·1	0·2	0·2	*0·1*	0·4	0·6	*0·1*	0·1	0·0	*0·0*	0·0	0·2	*0·1*	0·0	0·0	*0·0*
·0	0·0	0·1	*0·0*	0·5	0·8	*0·2*	0·5	0·4	*0·7*	0·3	0·4	*0·2*	0·0	0·0	*0·0*
·9	5·7	21·0	*5·6*	71·2	25·0	*6·0*	10·9	6·8	*11·2*	18·8	12·5	*7·8*	2·4	3·2	*7·3*
·6	100·6	101·7	*27·3*	200·7	187·6	*45·1*	2·2	5·5	*9·1*	32·6	31·7	*19·8*	0·0	0·7	*1·6*
·6	25·3	22·9	*6·1*	24·0	22·2	*5·3*	0·0	0·2	*0·3*	13·5	13·8	*8·6*	0·0	3·8	*8·7*
·8	4·4	6·4	*1·7*	2·0	2·1	*0·5*	0·0	0·0	*0·0*	1·1	1·2	*0·7*	0·0	0·0	*0·0*
·0	0·7	1·6	*0·4*	3·1	3·2	*0·8*	0·0	0·0	*0·0*	0·1	0·1	*0·1*	0·0	0·0	*0·0*
·4	4·0	3·4	*0·9*	4·1	3·9	*0·9*	0·3	0·4	*0·7*	1·0	0·8	*0·5*	0·0	0·0	*0·0*
·4	10·6	6·5	*1·7*	3·3	3·8	*0·9*	0·6	0·5	*0·8*	2·8	1·3	*0·8*	0·0	0·2	*0·5*
·0	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*
·3	1·6	1·5	*0·4*	1·6	0·7	*0·2*	0·1	0·0	*0·0*	0·0	0·1	*0·1*	2·4	0·9	*2·1*
·8	332·1	373·0	*99·9*	499·3	416·6	*99·9*	52·6	60·5	*100·0*	157·0	160·3	*99·9*	46·8	43·6	*99·9*

toni and *P. pulchella*, and apparently as yet undescribed,

APPEND

ZONE

	Dec., 1939–Jan., 1940. Mean No.	Est. No.	Est. %	April, 1940. Mean No.	Est. No.	Est. %	June, 1940. Mean No.	Est. No.	Est. %	August, 1940. Mean No.	Est. No.	E %
Hydropsyche	..	4·9	*1·3*	..	4·6	*1·2*	3·0	2·5	*0·6*	4·5	2·1	*0*
Rhyacophilidae larvæ	..	3·0	*0·8*	..	1·6	*0·4*	4·0	2·5	*0·6*	3·5	4·0	*0*
„ pupæ	..	0·0	*0·0*	..	0·7	*0·2*	0·7	0·6	*0·1*	2·0	1·9	*0*
Helicopsyche	..	133·3	*35·1*	..	141·4	*38·3*	220·2	227·7	*51·3*	405·0	245·2	*45*
Olinga larvæ	..	3·3	*0·9*	..	10·0	*2·7*	3·0	10·3	*2·3*	39·2	19·6	*4*
Sericostomatidæ—												
Type "C" larvæ	..	54·7	*14·4*	..	35·7	*9·6*	35·0	61·3	*13·8*	55·0	42·1	*8*
„ pupæ	..	0·7	*0·2*	..	0·2	*0·1*	0·2	0·1	*0·0*	6·7	1·7	*0*
Pycnocentrodes larvæ	..	98·2	*25·8*	..	45·3	*12·2*	138·0	69·2	*15·6*	90·7	81·7	*16*
„ pupæ	..	0·1	*0·0*	..	0·3	*0·1*	0·0	0·0	*0·0*	0·0	0·0	*0*
Coloburiscus	..	0·8	*0·2*	..	2·2	*0·6*	0·2	1·7	*0·4*	3·0	1·1	*0*
Deleatidium	..	15·7	*4·1*	..	49·0	*13·3*	25·2	35·3	*7·9*	75·0	43·3	*8*
Leptoperlidæ	..	2·8	*0·7*	..	8·9	*2·4*	6·2	7·7	*1·7*	6·7	11·1	*2*
Parnidae imagines	..	1·0	*0·3*	..	0·2	*0·1*	0·2	0·1	*0·0*	0·0	0·1	*0*
„ larvæ	..	53·9	*14·2*	..	42·3	*11·4*	6·8	5·2	*1·2*	45·5	5·2	*1*
Chironomidæ larvæ	..	0·1	*0·0*	..	2·5	*0·7*	7·7	3·8	*0·9*	11·7	17·3	*3*
„ pupæ	..	0·0	*0·0*	..	0·6	*0·2*	0·5	0·2	*0·0*	1·2	1·4	*0*
Simuliidae larvæ	..	0·0	*0·0*	..	0·0	*0·0*	0·5	0·2	*0·0*	0·0	0·2	*0*
„ pupæ	..	0·2	*0·1*	..	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0*
Other Diptera larvæ	..	0·5	*0·1*	..	0·5	*0·1*	1·5	0·6	*0·1*	1·2	1·6	*0*
Potamopyrgus	..	4·1	*1·1*	..	15·0	*4·1*	3·0	4·6	*1·0*	7·0	8·1	*1*
Latia	..	2·4	*0·6*	..	8·4	*2·3*	12·0	10·6	*2·4*	4·5	5·7	*1*
Oligochaeta	..	0·1	*0·0*	..	0·1	*0·0*	0·2	0·2	*0·0*	0·7	0·3	*0*
Total	..	379·8	*99·9*	..	369·5	*100·0*	468·1	444·4	*99·9*	763·1	493·7	*100*

ZONE

	Dec., 1939–Jan., 1940. Mean No.	Est. No.	Est. %	April, 1940. Mean No.	Est. No.	Est. %	June, 1940. Mean No.	Est. No.	Est. %	August, 1940. Mean No.	Est. No.	Es %
Hydropsyche	..	3·1	6·6	*2·4*	5·6	6·3	*1·8*	4·7	3·5	*0·8*	1·5	2·8	*0*
Rhyacophilidæ larvæ	..	1·1	1·8	*0·7*	1·4	0·9	*0·3*	1·2	1·5	*0·3*	2·7	2·4	*0*
pupæ	..	0·0	0·0	*0·0*	0·4	0·5	*0·1*	1·5	0·4	*0·1*	0·7	1·5	*0*
Helicopsyche	..	119·2	169·0	*62·0*	241·6	179·4	*50·2*	396·5	290·5	*66·8*	321·2	315·8	*61*
Olinga larvæ	..	2·1	2·4	*0·9*	12·7	7·1	*2·0*	11·0	7·2	*1·7*	5·7	13·6	*2*
Sericostomatidæ—													
Type "C" larvæ	..	5·1	30·5	*11·2*	19·3	28·2	*7·9*	22·0	34·1	*7·8*	13·0	23·8	*4*
„ pupæ	..	1·7	0·9	*0·3*	0·2	0·3	*0·1*	0·5	0·1	*0·0*	0·7	1·9	*0*
Pycnocentrodes larvæ	..	6·9	12·2	*4·5*	10·2	5·6	*1·6*	10·7	8·5	*2·0*	8·7	10·1	*2*
„ pupæ	..	0·6	0·0	*0·0*	0·1	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0*
Coloburiscus	..	2·0	1·2	*0·4*	3·7	3·3	*0·9*	2·0	2·5	*0·6*	1 2	1·6	*0*
Deleatidium	..	16·1	28·1	*10·3*	94·3	87·5	*24·5*	88·0	63·1	*14·5*	67·5	77·2	*15*
Leptoperlidæ	..	0·2	0·3	*0·1*	0·1	0·8	*0·2*	0·0	0·8	*0·2*	0·7	1·2	*0*
Parnidæ imagines	..	0·9	1·3	*0·5*	0·1	0·3	*0·1*	0·2	0·1	*0·0*	0·2	0·1	*0*
„ larvæ	..	3·2	12·1	*4·5*	19·3	9·8	*2·7*	1·0	1·2	*0·3*	1·2	1·2	*0*
Chironomidæ larvæ	..	0·5	0·4	*0·1*	7·1	6·3	*1·8*	6·0	9·1	*2·2*	37·0	43·3	*8*
„ pupæ	..	0·0	0·0	*0·0*	8·3	2·7	*0·8*	0·2	0·9	*0·2*	3·7	5·8	*1*
Simuliidæ larvæ	..	0·1	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·1	*0·0*	0·0	0·1	*0*
„ pupæ	..	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0*
Other Diptera larvæ	..	0·7	0·7	*0·3*	0·7	0·7	*0·2*	0·0	0·9	*0·2*	0·7	2·3	*0*
Potamopyrgus	..	1·7	3·4	*1·2*	20·4	12·6	*3·5*	5·0	3·8	*0·9*	5·7	6·9	*1*
Latia	..	2·1	1·4	*0·5*	5·9	4·9	*1·4*	6·0	6·1	*1·4*	1·7	3·3	*0*
Oligochaeta	..	0·0	0·2	*0·1*	1·1	0·2	*0·1*	0·7	0·3	*0·1*	0·2	0·6	*0*
Total	..	167·3	272·8	*100·0*	452·5	357·4	*100·2*	557·2	435·0	*99·9*	474·0	515·5	*99*

IX I

III

st.	October, 1940. Mean No.	Est. No.	Est. %	December, 1940. Mean No.	Est. No.	Est. %	February, 1941. Mean No.	Est. No.	Est. %	April, 1941. Mean No.	Est. No.	Est. %	October, 1941. Mean No.	Est. No.	Est. %
·1	0·9	2·2	*0·5*	1·5	3·1	*0·9*	4·0	2·5	*1·5*	1·5	3·0	*0·8*	..	0·7	*0·6*
·8	4·4	2·9	*0·6*	0·7	4·1	*1·2*	0·5	0·2	*0·1*	0·0	0·3	*0·1*	..	0·2	*0·2*
·1	1·0	1·8	*0·4*	1·2	1·6	*0·5*	0·2	0·1	*0·1*	0·2	0·4	*0·1*	..	0·1	*0·1*
·7	254·0	235·2	*51·9*	107·0	132·0	*39·2*	135·7	110·1	*67·5*	254·2	224·8	*60·8*	..	64·5	*55·9*
·0	6·5	13·4	*2·9*	3·2	11·1	*3·3*	3·2	2·8	*1·7*	3·5	4·2	*1·1*	..	3·6	*3·1*
·5	18·8	27·9	*6·2*	6·8	20·8	*6·2*	7·5	26·1	*16·0*	54·5	55·5	*15·0*	..	13·8	*12·0*
·3	0·0	5·3	*1·2*	1·2	2·3	*0·7*	0·0	0·2	*0·1*	0·4	0·2	*0·1*	..	0·0	*0·0*
·5	58·4	90·1	*19·8*	21·7	74·1	*22·0*	5·5	5·6	*3·4*	25·0	25·5	*6·9*	..	14·7	*12·7*
·0	0·6	0·1	*0·0*	0·0	0·2	*0·1*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	..	0·0	*0·0*
·2	0·3	0·8	*0·2*	0·7	1·1	*0·3*	0·2	0·0	*0·0*	0·5	0·8	*0·2*	..	0·3	*0·3*
·8	33·8	34·8	*7·7*	13·0	38·9	*11·6*	14·0	8·6	*5·3*	24·7	31·5	*8·5*	..	10·5	*9·1*
·2	3·0	4·0	*0·9*	5·5	8·9	*2·6*	1·7	2·7	*1·7*	7·7	11·3	*3·1*	..	2·1	*1·8*
·0	0·7	0·1	*0·0*	0·5	1·0	*0·3*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	..	0·0	*0·0*
·1	22·5	18·0	*4·0*	2·2	21·3	*6·3*	6·5	2·4	*1·5*	1·5	4·5	*1·2*	..	3·5	*3·0*
·5	8·7	5·4	*1·2*	3·5	9·9	*2·9*	0·5	0·3	*0·2*	1·2	1·6	*0·4*	..	0·0	*0·0*
·3	0·3	0·5	*0·1*	0·2	0·5	*0·1*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	..	0·0	*0·0*
·0	0·0	0·2	*0·0*	0·2	0·1	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	..	0·0	*0·0*
·0	0·0	0·1	*0·0*	0·2	0·1	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	..	0·0	*0·0*
·3	1·9	2·2	*0·5*	2·7	2·5	*0·7*	0·0	0·3	*0·2*	1·0	0·7	*0·2*	..	0·1	*0·1*
·7	18·7	5·8	*1·3*	2·0	3·4	*1·0*	2·7	0·6	*0·4*	0·5	1·6	*0·4*	..	0·3	*0·3*
·2	1·7	2·5	*0·6*	0·0	0·1	*0·0*	0·2	0·4	*0·2*	3·5	3·4	*0·9*	..	0·0	*0·0*
·1	0·0	0·3	*0·1*	0·0	0·1	*0·0*	0·7	0·2	*0·1*	0·2	0·6	*0·2*	..	0·9	*0·8*
·0	436·2	453·6	*100·3*	174·0	337·2	*99·9*	183·1	163·1	*100·0*	380·1	369·9	*100·0*	..	115·3	*100·0*

IV

t.	October, 1940. Mean No.	Est. No.	Est. %	December, 1940. Mean No.	Est. No.	Est. %	February, 1941. Mean No.	Est. No.	Est. %	April, 1941. Mean No.	Est. No.	Est. %	October, 1941. Mean No.	Est. No.	Est. %
·5	3·0	2·9	*0·7*	3·7	4·3	*1·3*	10·0	9·2	*8·3*	9·2	10·9	*1·5*	1·8	1·9	*1·2*
·4	1·7	1·7	*0·1*	2·9	2·4	*0·7*	1·2	0·6	*0·5*	0·2	0·8	*0·3*	1·3	1·4	*0·9*
·3	0·7	1·3	*0·3*	0·5	1·0	*0·3*	0·2	0·1	*0·1*	0·2	0·4	*0·2*	0·0	0·0	*0·0*
·3	325·0	302·0	*68·1*	234·0	168·7	*52·9*	83·0	53·3	*48·0*	109·2	108·7	*41·9*	127·1	107·4	*68·0*
·7	8·2	9·3	*2·1*	13·2	7·8	*2·4*	0·5	1·0	*0·9*	2·0	1·5	*0·6*	2·1	2·1	*1·3*
·6	18·7	15·6	*3·5*	4·5	11·5	*3·6*	13·0	32·8	*29·5*	57·2	69·6	*28·7*	4·9	7·1	*4·5*
·4	5·7	6·3	*1·4*	1·7	2·7	*0·8*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*
·0	12·2	11·2	*2·5*	8·2	9·2	*2·9*	0·5	0·8	*0·7*	4·0	3·6	*1·5*	1·3	1·3	*0·8*
·0	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*
·3	1·7	1·2	*0·3*	0·7	1·7	*0·5*	0·2	0·1	*0·1*	0·7	1·0	*0·4*	2·4	2·9	*1·8*
·0	51·0	62·2	*11·0*	63·0	69·4	*21·8*	12·2	10·6	*9·5*	36·5	38·6	*15·9*	32·7	33·0	*20·9*
·2	0·0	0·3	*0·1*	1·2	0·8	*0·3*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*
·0	0·2	0·1	*0·0*	1·0	1·3	*0·4*	0·2	0·1	*0·1*	0·0	0·1	*0·0*	0·0	0·0	*0·0*
·2	1·2	4·1	*0·9*	15·7	4·9	*1·5*	2·2	2·0	*1·8*	4·8	3·6	*1·5*	0·0	0·0	*0·0*
·4	30·2	13·5	*3·0*	10·0	24·8	*7·8*	1·0	0·3	*0·3*	1·2	2·1	*0·9*	0·0	0·0	*0·0*
·1	3·2	2·0	*0·5*	3·0	2·0	*0·6*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*
·0	0·2	0·1	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*
·0	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*
·4	4·2	3·0	*0·7*	5·2	3·4	*1·1*	0·0	0·2	*0·2*	0·5	0·3	*0·1*	0·0	0·0	*0·0*
·3	13·2	4·9	*1·1*	3·5	2·9	*0·9*	0·7	0·1	*0·1*	0·2	0·5	*0·2*	1·2	0·1	*0·1*
·6	2·5	1·5	*0·3*	0·2	0·1	*0·0*	0·2	0·0	*0·0*	0·0	0·2	*0·1*	0·0	0·0	*0·0*
·1	0·7	0·6	*0·1*	0·7	0·3	*0·1*	0·0	0·0	*0·0*	0·2	0·2	*0·1*	0·8	0·6	*0·4*
·8	483·5	443·8	*100·0*	371·4	319·2	*99·9*	125·1	111·2	*100·1*	226·1	242·1	*99·9*	175·9	157·8	*99·9*

APPENI

ZONE

	Dec., 1939–Jan., 1940. Mean No.	Est. No.	Est. %	April, 1940. Mean No.	Est. No.	Est. %	June, 1940. Mean No.	Est. No.	Est. %	August, 1940. Mean No.	Est. No.	Es %
Hydropsyche	1·7	9·3	*2·4*	11·9	8·8	*2·0*	2·3	4·8	*1·1*	2·8	4·0	*0*
Rhyacophilidæ larvæ	1·6	3·1	*0·8*	1·1	1·6	*0·4*	1·8	2·6	*0·6*	4·5	4·2	*0*
„ pupæ	0·0	0·0	*0·0*	0·6	0·7	*0·2*	0·0	0·6	*0·1*	2·9	2·1	*0*
Helicopsyche	233·2	126·0	*33·1*	115·4	133·7	*30·0*	196·3	208·0	*46·0*	217·6	235·0	*44*
Olinga larvæ	4·5	4·8	*1·3*	10·9	14·7	*3·3*	11·7	14·8	*3·3*	22·4	28·0	*5*
Sericostomatidæ—												
Type " C " larvæ	54·3	51·8	*13·6*	17·9	33·9	*7·6*	44·2	58·1	*12·9*	11·4	40·0	*7*
„ pupæ	0·4	1·9	*0·5*	0·5	0·6	*0·1*	0·0	0·3	*0·1*	0·0	4·4	*0*
Pycnocentrodes larvæ	43·7	76·6	*20·2*	22·2	35·3	*7·9*	25·0	53·9	*11·9*	32·2	63·8	*12*
„ pupæ	0·0	0·3	*0·1*	0·2	0·6	*0·1*	0·0	0·0	*0·0*	0·0	0·0	*0*
Coloburiscus	4·4	5·2	*1·4*	12·9	14·6	*3·3*	3·2	4·2	*0·9*	1·6	2·7	*0*
Deleatidium	26·7	24·4	*6·4*	96·2	114·2	*25·6*	83·2	77·7	*17·2*	74·3	95·3	*17*
Leptoperlidæ	0·3	0·5	*0·1*	1·0	1·3	*0·3*	0·0	1·1	*0·2*	2·3	1·6	*0*
Parnidæ imagines	0·4	0·9	*0·2*	0·8	0·2	*0·0*	0·0	0·1	*0·0*	0·0	0·1	*0*
„ larvæ	7·5	64·6	*17·0*	12·7	50·7	*11·3*	9·5	6·2	*1·4*	9·5	6·2	*1*
Chironomidæ larvae	0·8	0·2	*0·1*	12·7	2·7	*0·6*	2·5	4·1	*0·9*	15·2	18·8	*3*
„ pupæ	0·0	0·0	*0·0*	6·4	1·8	*0·4*	0·4	0·6	*0·1*	4·5	4·1	*0*
Simuliidæ larvæ	0·0	0·0	*0·0*	0·3	0·0	*0·0*	1·0	0·3	*0·1*	0·0	0·3	*0*
„ pupæ	0·3	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0*
Other Diptera larvæ	1·4	1·1	*0·3*	0·2	1·1	*0·2*	1·0	1·4	*0·3*	2·5	3·9	*0*
Potamopyrgus	2·0	7·1	*1·9*	7·2	26·2	*5·9*	10·0	8·0	*1·8*	8·7	14·2	*2*
Latia	0·1	0·8	*0·2*	1·7	2·7	*0·6*	1·6	3·4	*0·8*	4·4	1·8	*0*
Oligochaeta	2·7	1·2	*0·3*	1·2	1·2	*0·3*	3·3	1·8	*0·4*	6·5	3·5	*0*
Total	386·0	379·8	*99·9*	334·0	446·6	*100·1*	427·0	452·0	*100·1*	423·3	534·0	*100*

DIX I

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t.	October, 1940. Mean No.	Est. No.	Est. %	December, 1940. Mean No.	Est. No.	Est. %	February, 1941. Mean No.	Est. No.	Est. %	April, 1941. Mean No.	Est. No.	Est. %	October, 1941. Mean No.	Est. No.	Est. %
·7	10·6	4·1	*0·8*	2·3	6·0	*1·6*	5·5	5·5	*3·7*	6·0	6·5	*1·9*	2·3	2·4	*1·6*
·8	4·9	3·0	*0·6*	1·8	4·3	*1·1*	0·9	0·7	*0·5*	0·9	1·2	*0·3*	0·4	0·4	*0·3*
4	1·8	2·0	*0·4*	0·4	1·6	*0·4*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*
·1	358·5	225·2	*45·0*	182·6	125·5	*33·1*	65·6	75·6	*50·8*	208·0	154·3	*45·0*	81·9	68·8	*45·9*
2	31·4	19·2	*3·9*	13·3	15·9	*4·2*	0·0	0·2	*0·1*	0·5	0·3	*0·1*	2·1	2·1	*1·4*
·4	14·9	26·4	*5·3*	31·5	19·7	*5·2*	30·5	28·7	*19·3*	32·8	60·8	*17·7*	13·6	19·2	*12·8*
8	14·1	13·9	*2·8*	5·6	6·0	*1·6*	5·2	4·3	*2·9*	0·7	3·1	*0·9*	0·0	0·0	*0·0*
0	90·2	70·2	*14·2*	92·2	57·7	*15·2*	5·5	3·3	*2·2*	12·0	14·7	*4·3*	20·1	20·6	*13·7*
0	0·9	0·2	*0·0*	0·0	0·4	*0·1*	0·5	0·2	*0·1*	0·0	0·1	*0·0*	0·0	0·0	*0·0*
5	2·4	2·0	*0·4*	2·8	3·0	*0·8*	0·4	0·0	*0·0*	0·0	0·5	*0·1*	2·0	2·4	*1·6*
9	104·5	76·6	*15·6*	68·8	85·6	*22·6*	19·8	23·4	*15·8*	87·8	85·5	*24·8*	19·8	20·1	*13·4*
3	0·0	0·6	*0·1*	0·6	1·3	*0·3*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·3	0·5	*0·3*
0	0·0	0·1	*0·0*	1·3	0·9	*0·2*	0·0	0·3	*0·2*	0·6	0·3	*0·1*	0·0	0·0	*0·0*
·2	68·2	21·5	*4·3*	16·6	25·5	*6·7*	6·3	4·3	*2·9*	9·5	7·9	*2·3*	15·1	10·6	*7·1*
·5	7·8	5·9	*1·2*	9·4	10·8	*2·9*	5·7	1·1	*0·7*	0·8	6·2	*1·8*	0·8	0·9	*0·6*
·8	1·2	1·4	*0·3*	0·4	1·4	*0·4*	0·5	0·0	*0·0*	0·0	0·0	*0·0*	0·4	0·0	*0·0*
·1	0·0	0·3	*0·1*	0·0	0·1	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*
·0	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*
·7	5·0	5·3	*1·1*	9·0	6·0	*1·6*	1·1	0·4	*0·3*	0·0	0·7	*0·2*	0·5	0·5	*0·3*
·6	31·2	10·1	*2·0*	10·0	5·9	*1·6*	1·2	0·4	*0·3*	1·2	1·1	*0·3*	3·7	0·2	*0·1*
·3	0·0	0·8	*0·2*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*	0·0	0·0	*0·0*
·7	2·6	2·8	*0·6*	0·0	1·5	*0·4*	0·5	0·2	*0·1*	0·2	0·4	*0·1*	1·6	1·2	*0·8*
·0	750·2	491·6	*99·9*	448·6	379·1	*100·0*	149·2	148·6	*99·9*	361·0	343·6	*99·9*	164·6	149·9	*99·9*

APPEND

Summarized gravimetric results of the faunistic collections; showin
form, the mean individual dry weight, the estimated wet weight pe
in the estimated mean fauna. Results for each zone t

ZONE

	Dec., 1939–Jan., 1940. Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	April, 1940. Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	June, 1940. Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	August, 1940. Mean Dry Wt.	Total Wet Wt.	We Wt %
Hydropsyche	*1·20*	43·9	*9·1*	*1·42*	50·6	*6·7*	*2·06*	40·0	*8·0*	*2·18*	34·5	*3·*
Rhyacophilidæ larvæ	*1·59*	15·7	*3·2*	*2·64*	13·2	*1·8*	*2·16*	18·4	*3·7*	*3·48*	48·4	*5·*
,, pupæ	..	..	..	*3·87*	15·7	*2·1*	*3·87*	12·2	*2·4*	*3·87*	45·3	*5·*
Helicopsyche	1·24	2·4	*0·5*	0·83	1·7	*0·2*	0·65	2·1	*0·4*	1·44	5·1	*0·*
Olinga larvæ	*1·63*	1·8	*0·4*	*1·63*	5·5	*0·7*	*1·63*	5·7	*1·1*	*1·63*	1·1	*0·*
Sericostomatidæ—												
Type " C " larvæ	*0·84*	0·9	*0·2*	*0·28*	0·2	*0·0*	*0·48*	0·6	*0·1*	*1·21*	1·0	*0·*
,, pupæ	*1·61*	0·1	*0·0*	*1·61*	0·1	*0·0*	..	..	..	*1·61*	0·2	*0·*
Pycnocentrodes larvæ	1·17	31·4	*6·5*	0·31	3·8	*0·5*	0·28	5·5	*1·1*	0·50	11·6	*1·*
,, pupæ	*4·81*	6·3	*1·3*	*4·81*	15·7	*2·1*	..	..	..	..	..	..
Coloburiscus	*2·27*	10·7	*2·2*	*0·83*	10·7	*1·4*	*1·32*	12·9	*2·6*	*0·66*	3·8	*0·*
Deleatidium	0·64	83·5	*17·3*	0·50	203·3	*27·1*	0·36	105·6	*21·0*	0·74	265·8	*29·*
Leptoperlidæ	*0·10*	0·0	*0·0*	*0·10*	0·2	*0·0*	*0·82*	0·9	*0·2*	*1·11*	1·6	*0·*
Parnidæ imagines	*0·40*	3·6	*0·7*	*0·40*	0·7	*0·1*	*0·40*	0·3	*0·1*	*0·40*	0·3	*0·*
,, larvæ	0·16	134·5	*27·8*	0·28	184·8	*24·6*	0·54	43·6	*8·7*	0·29	23·3	*2·*
Chironomidæ larvæ	0·10	0·5	*0·1*	0·04	3·5	*0·5*	0·05	6·4	*1·3*	0·14	85·0	*9·*
,, pupæ	..	..	..	*0·07*	4·2	*0·6*	*0·13*	2·5	*0·5*	*0·18*	24·0	*2·*
Simuliidæ larvæ	*0·19*	0·2	*0·0*	*0·19*	0·3	*0·0*	*0·19*	1·9	*0·4*	*0·19*	1·9	*0·*
,, pupæ	0·29	0·4	*0·1*	..	..	..	*0·29*	0·2	*0·0*	*0·29*	0·2	*0·*
Other Diptera larvæ	*1·81*	5·7	*1·2*	*2·06*	6·5	*0·9*	*1·48*	5·7	*1·1*	*1·51*	15·8	*1·*
Potamopyrgus	0·77	62·5	*12·9*	0·49	145·8	*19·4*	1·24	112·8	*22·5*	0·61	98·8	*10·*
Latia	*2·06*	0·2	*0·0*	*0·45*	0·2	*0·0*	*0·11*	0·1	*0·0*	*0·25*	0·1	*0·*
Oligochaeta	*5·53*	79·7	*16·4*	*5·53*	84·0	*11·2*	*5·53*	124·0	*24·8*	*5·53*	246·0	*27·*
Total	..	484·0	*99·9*	..	750·7	*99·9*	..	501·4	*100·0*	..	913·8	*100·*

ZONE

	Dec., 1939–Jan., 1940. Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	April, 1940. Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	June, 1940. Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	August, 1940. Mean Dry Wt.	Total Wet Wt.	We Wt %
Hydropsyche	*1·20*	37·3	*13·7*	*1·42*	41·4	*9·9*	*2·06*	32·6	*10·7*	*2·18*	28·2	*4·*
Rhyacophilidæ larvæ	*1·25*	22·5	*8·3*	*2·09*	19·8	*4·7*	*1·70*	25·2	*8·3*	*2·74*	65·5	*9·*
,, pupæ	..	..	..	*4·28*	31·0	*7·4*	*4·28*	23·2	*7·6*	*4·28*	87·3	*13·*
Helicopsyche	*0·82*	14·4	*5·3*	*0·48*	9·1	*2·2*	0·62	19·1	*6·3*	0·60	19·9	*2·*
Olinga larvæ	*1·50*	2·9	*1·1*	*1·50*	8·8	*2·1*	*1·50*	9·2	*3·0*	*1·50*	17·4	*2·*
Sericostomatidæ—												
Type " C " larvæ	*0·69*	12·8	*4·7*	*0·22*	2·7	*0·6*	*0·39*	8·4	*2·8*	0·86	12·5	*1·*
,, pupæ	*1·61*	1·0	*0·4*	*1·61*	0·3	*0·1*	*1·61*	0·1	*0·0*	*1·61*	2·7	*0·*
Pycnocentrodes larvæ	*1·23*	31·6	*11·6*	*0·35*	4·3	*1·0*	0·26	4·9	*1·6*	0·49	10·6	*1·*
,, pupæ	*4·81*	5·4	*2·0*	*4·81*	14·1	*3·4*	..	..	..	..	..	..
Coloburiscus	*2·27*	36·3	*13·4*	*0·83*	36·7	*8·8*	*1·32*	21·1	*6·9*	*0·66*	6·9	*1·*
Deleatidium	*0·62*	56·7	*20·9*	*0·56*	159·5	*38·1*	0·48	98·4	*32·4*	0·62	156·0	*23·*
Leptoperlidæ	*0·10*	0·1	*0·0*	*0·88*	2·0	*0·5*	*0·82*	1·2	*0·4*	*1·11*	3·3	*0·*
Parnidæ imagines	*0·40*	0·6	*0·2*	*0·40*	0·1	*0·0*	*0·40*	0·1	*0·0*	*0·40*	0·1	*0·*
,, larvæ	*0·18*	22·8	*8·4*	*0·29*	28·7	*6·8*	0·52	6·3	*2·1*	0·37	4·5	*0·*
Chironomidæ larvæ	*0·12*	1·9	*0·7*	*0·07*	18·1	*4·3*	0·08	14·0	*4·6*	0·12	144·1	*21·*
,, pupæ	..	..	..	*0·07*	10·3	*2·5*	*0·13*	6·6	*2·2*	*0·18*	58·8	*8·*
Simuliidæ larvæ	*0·19*	0·4	*0·1*	*0·19*	0·6	*0·1*	*0·19*	4·3	*1·4*	*0·19*	4·2	*0·*
,, pupæ	*0·29*	1·0	*0·4*	..	..	..	*0·29*	0·4	*0·1*	*0·29*	0·4	*0·*
Other Diptera larvæ	*1·05*	2·6	*1·0*	*1·19*	2·9	*0·7*	*0·85*	2·7	*0·9*	*0·96*	8·4	*1·*
Potamopyrgus	*0·98*	8·6	*3·2*	*0·49*	15·1	*3·6*	0·75	7·3	*2·4*	0·26	4·5	*0·*
Latia	..	..	..	*0·45*	0·1	*0·0*	..	..	..	..	..	..
Oligochaeta	*5·53*	12·6	*4·6*	*5·53*	12·6	*3·0*	*5·53*	18·9	*6·2*	*5·53*	35·7	*5·*
Total	..	271·5	*100·0*	..	418·2	*99·8*	..	304·0	*99·9*	..	671·0	*100·*

X II

for each month in which collections were made and for each square foot for the whole zone, and the percentage by weight bulated separately. All weights expressed in mg.

I

October, 1940. Mean Dry Wt.	October, 1940. Total Wet Wt.	October, 1940. Wet Wt. %	December, 1940. Mean Dry Wt.	December, 1940. Total Wet Wt.	December, 1940. Wet Wt. %	February, 1941. Mean Dry Wt.	February, 1941. Total Wet Wt.	February, 1941. Wet Wt. %	April, 1941. Mean Dry Wt.	April, 1941. Total Wet Wt.	April, 1941. Wet Wt. %	October, 1941. Mean Dry Wt.	October, 1941. Total Wet Wt.	October, 1941. Wet Wt. %
1·73	28·7	4·3	0·60	14·5	2·5	0·60	14·9	11·1	2·06	60·6	13·9	1·97	18·4	12·6
2·16	20·3	3·1	2·25	31·4	5·5	1·07	5·8	4·3	1·47	11·2	2·6	0·79	1·4	1·0
3·87	41·8	6·3	3·87	34·8	6·1	3·87	7·0	5·2	3·87	17·4	4·0	3·87	7·0	4·8
1·55	5·3	0·8	3·59	6·8	1·2	0·99	1·0	0·7	0·61	1·2	0·3	0·58	1·8	1·2
1·63	7·2	1·1	1·63	5·9	1·0	1·63	1·8	1·3	1·63	2·6	0·6	1·63	1·2	0·8
0·79	0·4	0·1	0·86	0·3	0·1	0·23	0·0	0·0	0·28	0·4	0·1	0·39	1·1	0·8
1·61	0·9	0·1	1·61	0·4	0·1	..	..	..	..	..	..	..	..	..
1·07	26·6	4·0	2·74	56·6	9·9	1·02	1·9	1·4	0·30	2·6	0·6	0·37	0·5	0·3
4·81	6·4	1·0	4·81	9·6	1·7	4·81	0·6	0·4	4·81	0·3	0·1	..	..	..
3·23	15·1	2·3	1·77	11·7	2·1	1·72	7·4	5·5	1·01	63·4	14·6	3·28	55·0	37·6
0·38	109·4	16·6	0·29	93·2	16·2	0·13	14·3	10·6	0·23	92·3	21·3	0·30	28·6	19·6
0·58	0·2	0·0	0·38	0·6	0·1	0·22	0·3	0·2	0·39	2·8	0·6	..	..	..
0·40	0·3	0·0	0·40	3·6	0·6	0·40	0·2	0·1	0·40	0·2	0·0	..	..	..
0·22	61·6	9·3	0·37	122·5	21·4	0·19	20·5	15·2	0·35	69·2	15·9	0·15	6·1	4·2
0·11	20·6	3·1	0·05	16·6	2·9	0·02	0·3	0·2	0·04	4·0	0·9	..	..	..
0·08	3·6	0·5	0·06	2·6	0·5	..	..	..	0·08	0·4	0·1	..	..	..
0·19	2·3	0·3	0·19	0·8	0·1	0·19	0·1	0·1	0·19	0·7	0·2	..	..	..
0·29	1·3	0·2	0·29	2·4	0·4	..	..	..	..	..	..	..	..	..
0·91	12·7	1·9	0·71	11·2	1·9	0·45	1·9	1·4	1·31	11·4	2·6	..	..	..
0·70	92·8	14·0	0·65	44·5	7·7	1·51	35·6	26·5	0·32	20·5	4·7	0·53	6·3	4·3
0·06	0·0	0·0	..	..	..	..	..	..	0·31	0·1	0·0	..	..	..
5·53	203·7	30·8	5·53	102·9	18·0	5·53	21·0	15·6	5·53	73·5	16·9	5·53	18·9	12·9
..	661·2	99·8	..	572·9	100·0	..	134·6	99·8	..	434·8	100·0	..	146·3	100·1

II

October, 1940. Mean Dry Wt.	October, 1940. Total Wet Wt.	October, 1940. Wet Wt. %	December, 1940. Mean Dry Wt.	December, 1940. Total Wet Wt.	December, 1940. Wet Wt. %	February, 1941. Mean Dry Wt.	February, 1941. Total Wet Wt.	February, 1941. Wet Wt. %	April, 1941. Mean Dry Wt.	April, 1941. Total Wet Wt.	April, 1941. Wet Wt. %	October, 1941. Mean Dry Wt.	October, 1941. Total Wet Wt.	October, 1941. Wet Wt. %
1·72	23·7	6·0	0·60	11·9	2·7	0·60	5·4	10·5	2·06	21·5	15·4	1·97	2·3	3·6
1·70	29·1	7·3	1·78	43·3	9·6	0·84	0·8	1·6	1·17	1·1	0·8	0·62	1·1	1·7
4·28	81·4	20·5	4·28	65·8	15·0	4·28	7·7	15·0	4·28	17·4	12·5	4·28	1·9	2·9
1·09	34·5	8·7	2·62	45·8	10·4	0·72	2·3	4·5	0·69	4·6	3·3	0·56	2·0	3·1
1·50	11·5	2·9	1·50	9·9	2·2	1·50	17·8	34·6	1·50	2·5	1·8	1·50	0·5	0·8
0·56	5·4	1·4	0·77	5·3	1·1	0·35	2·2	4·3	0·21	2·7	1·9	0·47	2·5	3·9
1·61	8·6	2·2	1·61	3·7	0·8	1·61	1·3	2·5	1·61	1·0	0·7	..	..	..
0·68	15·9	4·0	2·26	43·6	9·9	0·75	1·3	2·5	0·24	2·0	1·4	0·29	0·7	1·1
4·81	5·4	1·4	4·81	8·6	2·0	..	..	..	4·81	0·3	0·2	..	..	..
3·23	25·2	6·3	1·77	18·7	4·2	1·72	2·0	3·9	1·01	13·8	9·9	3·28	19·2	29·8
0·36	72·9	18·3	0·49	110·4	25·1	0·15	5·8	11·3	0·34	48·5	34·8	0·32	12·8	19·9
0·58	0·4	0·1	0·38	0·8	0·2	..	..	..	0·39	0·4	0·3	..	..	..
0·40	0·1	0·0	0·40	0·6	0·1	0·40	0·3	0·6	0·40	0·3	0·2	..	..	..
0·21	8·8	2·2	0·12	6·0	1·3	0·21	2·9	5·6	0·31	7·8	5·6	0·21	1·3	2·0
0·04	15·3	3·8	0·05	33·8	7·7	0·02	0·4	0·8	0·04	4·8	3·3	0·05	0·1	0·2
0·08	8·7	2·2	0·06	4·9	1·1	0·06	0·1	0·2	0·08	5·2	3·7	0·06	1·1	1·7
0·19	5·1	1·3	0·19	1·7	0·4	..	..	..	0·19	1·0	0·1	..	..	..
0·29	1·9	0·5	0·29	3·9	0·8	..	..	..	0·29	0·1	0·1	..	..	..
0·52	6·2	1·6	0·41	5·6	1·3	0·25	0·3	0·6	0·72	2·0	1·4	..	..	..
0·51	6·3	1·6	0·26	1·9	0·4	0·93	0·9	1·7	0·16	0·4	0·3	0·30	0·1	0·2
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
5·53	31·5	7·9	5·53	14·7	3·3	..	..	..	5·53	2·1	1·5	5·53	18·9	29·3
..	397·9	100·2	..	440·9	100·0	..	51·5	100·2	..	139·5	99·8	..	64·5	100·2

APPEN

ZONE

	Dec., 1939–Jan., 1940. Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	April, 1940. Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	June, 1940. Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	August, 194 Mean Dry Wt.	Total Wet Wt.
Hydropsyche	*1·20*	21·2	*10·6*	*1·42*	23·5	*9·1*	*2·06*	18·5	*9·0*	*2·18*	16·5
Rhyacophilidæ larvæ	*0·64*	8·6	*4·7*	*1·07*	7·7	*5·0*	*0·87*	9·0	*4·4*	*1·40*	25·2
„ pupæ	..	..	..	*2·91*	9·2	*5·6*	*2·91*	7·9	*5·9*	*2·91*	24·8
Helicopsyche	*0·55*	32·0	*17·5*	*0·32*	19·8	*7·7*	0·39	38·7	*18·8*	0·52	53·9
Olinga larvæ	*0·81*	3·2	*1·7*	*0·81*	9·7	*5·8*	*0·81*	10·0	*4·9*	*0·81*	19·0
Sericostomatidæ—											
Type "C" larvæ	*0·55*	14·8	*8·1*	*0·18*	3·2	*1·2*	0·35	10·4	*5·1*	1·01	21·0
„ pupæ	*1·61*	0·6	*0·3*	*1·61*	0·2	*0·1*	*1·61*	0·1	*0·0*	*1·61*	1·4
Pycnocentrodes larvæ	*0·36*	23·7	*13·0*	*0·10*	3·2	*1·2*	0·15	6·9	*3·4*	0·29	16·3
„ pupæ	*4·81*	0·3	*0·1*	*4·81*	1·0	*0·4*	..	..	..	..	..
Coloburiscus	*2·27*	7·1	*3·9*	*0·83*	7·1	*2·8*	*1·32*	8·7	*4·2*	*0·66*	2·8
Deleatidium	*0·56*	37·8	*20·7*	*0·50*	105·4	*40·9*	0·30	46·6	*22·7*	0·63	117·2
Leptoperlidæ	*0·10*	1·0	*0·5*	*0·88*	29·0	*11·3*	*0·82*	23·3	*11·3*	1·11	45·6
Parnidæ imagines	*0·40*	0·8	*0·4*	*0·40*	0·2	*0·1*	*0·40*	0·1	*0·0*	*0·40*	0·1
„ larvæ	*0·18*	19·4	*10·6*	*0·29*	24·5	*9·5*	0·31	3·2	*1·6*	0·39	4·1
Chironomidæ larvæ	..	..	..	*0·05*	0·4	*0·2*	0·04	0·6	*0·3*	0·06	3·8
„ pupæ	..	..	..	*0·07*	0·2	*0·1*	*0·13*	0·1	*0·0*	*0·18*	1·2
Simuliidæ larvæ	..	..	..	..	..	..	0·19	0·2	*0·1*	*0·19*	0·2
„ pupæ	*0·29*	0·2	*0·1*	..	..	..	..	..	..	..	..
Other Diptera larvæ	*0·68*	1·3	*0·7*	*0·77*	1·3	*0·5*	*0·56*	1·2	*0·6*	*0·56*	3·1
Potamopyrgus	*0·39*	3·0	*1·6*	*0·19*	5·4	*2·1*	0·21	1·8	*0·9*	0·20	3·1
Latia	*2·06*	5·7	*3·1*	*0·45*	4·4	*1·7*	*0·11*	13·8	*6·7*	*0·25*	1·6
Oligochaeta	*5·53*	2·1	*1·1*	*5·53*	2·1	*0·8*	*5·53*	4·2	*2·0*	*5·53*	6·3
Total	..	182·8	*99·7*	..	257·5	*100·1*	..	205·3	*99·9*	..	367·2

ZONE

	Dec., 1939–Jan., 1940. Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	April, 1940. Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	June, 1940. Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	August, 194 Mean Dry Wt.	Total Wet Wt.
Hydropsyche	*1·20*	28·4	*15·6*	*1·42*	32·2	*14·9*	*2·06*	25·8	*14·3*	*2·18*	21·8
Rhyacophilidae larvæ	*0·56*	4·5	*2·5*	*0·94*	3·8	*1·8*	*0·76*	5·1	*2·8*	*1·23*	13·3
„ pupæ	..	..	..	*3·07*	6·9	*3·2*	*3·07*	5·5	*3·0*	*3·07*	20·7
Helicopsyche	0·87	62·5	*34·3*	0·39	30·4	*14·1*	0·37	46·4	*25·6*	0·51	69·3
Olinga larvæ	*1·11*	3·2	*1·8*	*1·11*	9·5	*4·4*	*1·11*	9·6	*5·3*	*1·11*	18·1
Sericostomatidæ—											
Type "C" larvæ	0·70	10·7	*5·9*	0·16	2·2	*1·0*	0·33	5·4	*3·0*	0·61	7·1
„ pupæ	*1·61*	0·7	*0·4*	*1·61*	0·2	*0·1*	*1·61*	0·1	*0·1*	*1·61*	1·5
Pycnocentrodes larvæ	0·97	7·8	*4·3*	0·20	0·7	*0·3*	0·23	1·4	*0·8*	0·33	2·2
„ pupæ	..	..	..	..	..	..	..	..	..	..	..
Coloburiscus	*2·27*	10·6	*5·8*	*0·83*	10·7	*5·0*	*1·32*	12·8	*7·1*	*0·66*	4·1
Deleatidium	0·28	33·7	*18·5*	0·25	93·7	*43·4*	0·19	51·7	*28·6*	0·35	115·8
Leptoperlidæ	*0·10*	0·1	*0·1*	*0·88*	2·6	*1·2*	*0·82*	2·4	*1·3*	*1·11*	4·9
Parnidæ imagines	*0·40*	1·0	*0·5*	*0·40*	0·2	*0·1*	*0·40*	0·1	*0·1*	*0·40*	0·1
„ larvæ	0·23	5·7	*3·1*	0·28	5·5	*2·5*	*0·35*	0·8	*0·4*	*0·32*	0·8
Chironomidæ larvæ	*0·12*	0·2	*0·1*	0·07	1·6	*0·7*	0·08	2·8	*1·5*	0·04	6·5
„ pupæ	..	..	..	0·07	0·9	*0·4*	0·13	0·6	*0·3*	*0·18*	5·0
Simuliidæ larvæ	..	..	..	..	..	..	*0·19*	0·1	*0·0*	*0·19*	0·1
„ pupæ	..	..	..	..	..	..	..	..	..	..	..
Other Diptera larvæ	*0·67*	1·6	*0·9*	0·76	0·5	*0·2*	*0·55*	1·7	*0·9*	*0·56*	4·5
Potamopyrgus	*0·65*	4·2	*2·3*	0·35	7·7	*3·6*	0·19	1·4	*0·8*	0·14	1·9
Latia	*2·06*	3·3	*1·8*	*0·45*	2·5	*1·2*	*0·11*	0·8	*0·4*	*0·25*	1·0
Oligochaeta	*5·53*	4·2	*2·3*	*5·53*	4·2	*1·9*	*5·53*	6·3	*3·5*	*5·53*	12·6
Total	..	182·4	*100·2*	..	216·0	*100·0*	..	180·8	*100·0*	..	311·3

IX II

III

t	October, 1940. Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	December, 1940. Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	February, 1941. Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	April, 1941. Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	October, 1941. Mean Dry Wt.	Total Wet Wt.	Wet Wt. %
5	1·73	13·7	5·3	0·60	6·7	2·3	0·60	5·4	6·6	2·06	22·2	15·6	1·97	5·5	7·9
8	0·87	11·4	4·4	0·91	16·8	5·7	0·43	0·4	0·5	0·59	0·8	0·6	0·32	0·3	0·4
8	2·91	23·6	9·1	2·91	20·9	7·1	2·91	1·3	1·6	2·91	5·2	3·7	2·91	1·3	1·9
7	0·79	80·0	30·9	1·58	89·7	30·4	0·92	44·0	53·8	0·30	29·2	20·5	0·28	7·7	11·1
2	0·81	13·0	5·0	0·81	10·8	3·7	0·81	2·7	3·3	0·81	4·1	2·9	0·81	3·5	5·1
7	0·46	6·4	2·5	0·32	3·3	1·1	0·20	2·6	3·2	0·16	4·4	3·1	0·59	4·0	5·8
4	1·61	4·2	1·6	1·61	1·8	0·6	1·61	0·2	0·2	1·61	0·2	0·1	..	..	..
5	0·28	17·1	6·6	0·37	18·5	6·3	0·27	1·0	1·2	0·20	3·3	2·3	0·11	1·1	1·6
.	4·81	0·3	0·1	4·81	0·6	0·2	..	..	..	..	..	..	..	..	..
8	3·23	10·1	3·9	1·77	7·6	2·6	..	..	..	1·01	3·1	2·2	3·28	4·0	5·8
0	0·32	48·0	18·6	0·52	87·2	29·6	0·41	15·1	18·4	0·23	31·2	21·9	0·37	16·2	23·4
4	0·58	8·6	3·3	0·38	12·6	4·3	0·22	2·2	2·7	0·39	20·2	14·2	0·58	4·5	6·5
0	0·40	0·1	0·0	0·40	0·8	0·3	..	..	..	..	..	..	..	..	..
1	0·30	10·8	4·2	0·23	9·8	3·3	0·26	1·2	1·5	0·35	3·1	2·2	0·30	2·1	3·0
0	0·04	0·8	0·3	0·09	3·3	1·1	0·02	0·0	0·0	0·03	0·2	0·1	..	..	..
3	0·08	0·2	0·1	0·06	0·1	0·0	..	..	..	..	..	..	..	..	..
1	0·19	0·2	0·1	0·19	0·8	0·3	..	..	..	..	..	..	..	..	..
.	0·29	0·1	0·0	0·29	0·1	0·0	..	..	..	..	..	..	..	..	..
8	0·34	2·6	1·0	0·27	0·2	0·1	0·17	0·2	0·2	0·47	1·1	0·8	0·34	0·1	0·1
8	0·10	1·1	0·4	0·20	1·3	0·4	0·54	0·6	0·7	0·07	0·2	0·1	0·12	0·1	0·1
4	0·06	0·2	0·1	0·10	0·0	0·0	1·50	0·7	0·8	0·31	1·2	0·8	..	..	..
7	5·53	6·3	2·4	5·53	2·1	0·7	5·53	4·2	5·1	5·53	12·6	8·8	5·53	18·9	27·3
0	..	258·8	99·9	..	295·0	100·1	..	81·8	99·8	..	142·3	99·9	..	69·3	100·0

IV

et t. %	October, 1940. Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	December, 1940. Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	February, 1941. Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	April, 1941. Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	October, 1941. Mean Dry Wt.	Total Wet Wt.	Wet Wt. %
0	1·73	18·1	6·2	0·60	9·3	4·9	0·60	2·0	5·8	2·06	80·6	50·9	1·97	13·5	11·6
3	0·76	5·8	2·0	0·79	8·5	3·7	0·38	1·0	2·9	0·52	1·9	1·2	0·28	1·8	1·5
7	3·07	17·9	6·1	3·07	13·8	6·0	3·07	1·4	4·0	3·07	5·5	3·5	..	..	..
3	0·55	72·4	24·8	0·92	67·5	29·2	0·02	13·9	40·2	0·46	21·7	13·7	0·52	23·6	20·3
8	1·11	12·4	4·3	1·11	10·4	4·1	1·11	1·3	3·8	1·11	2·0	1·3	1·11	2·8	2·4
3	0·58	4·5	1·5	0·54	3·1	1·3	0·10	1·6	4·6	0·18	6·3	4·0	0·27	0·9	0·8
5	1·61	1·9	0·7	1·61	2·2	0·9	..	..	..	..	..	..	..	..	..
7	0·45	3·4	1·2	0·64	3·9	1·7	0·33	0·2	0·6	0·15	0·4	0·3	0·17	0·2	0·2
3	3·23	15·1	5·2	1·77	11·7	5·1	1·72	0·7	2·0	1·01	3·9	2·5	3·28	37·1	31·8
3	0·42	111·8	38·3	0·26	77·8	33·6	0·24	10·9	31·5	0·16	26·6	16·8	0·17	24·1	20·7
6	0·58	0·6	0·2	0·38	1·1	0·5	..	..	..	..	..	..	..	..	..
0	..	..	..	0·10	1·0	0·1	0·40	0·1	0·3	0·40	0·1	0·1	..	..	..
3	0·25	2·0	0·7	0·24	2·3	1·0	0·31	1·2	3·5	0·45	3·2	2·0	..	..	..
1	0·07	3·5	1·2	0·09	8·2	3·5	0·05	0·1	0·3	0·05	0·4	0·3	..	..	..
6	0·08	0·8	0·3	0·06	0·6	0·3	..	..	..	..	..	..	..	..	..
0	0·19	0·1	0·0	..	..	..	..	..	..	..	..	..	..	..	..
5	0·34	3·6	1·2	0·27	3·2	1·1	0·17	0·1	0·3	0·46	0·5	0·3	..	..	..
6	0·06	5·6	1·9	0·12	0·7	0·3	0·27	0·1	0·3	0·05	0·0	0·0	0·08	0·0	0·0
3	0·06	0·1	0·0	0·10	0·0	0·0	..	..	..	1·50	0·3	0·2	..	..	..
1	5·53	12·6	4·3	5·53	6·3	2·7	..	..	..	5·53	4·2	2·7	5·53	12·6	10·8
1	..	292·2	100·1	..	231·6	100·0	..	34·6	100·1	..	157·6	99·8	..	116·6	100·1

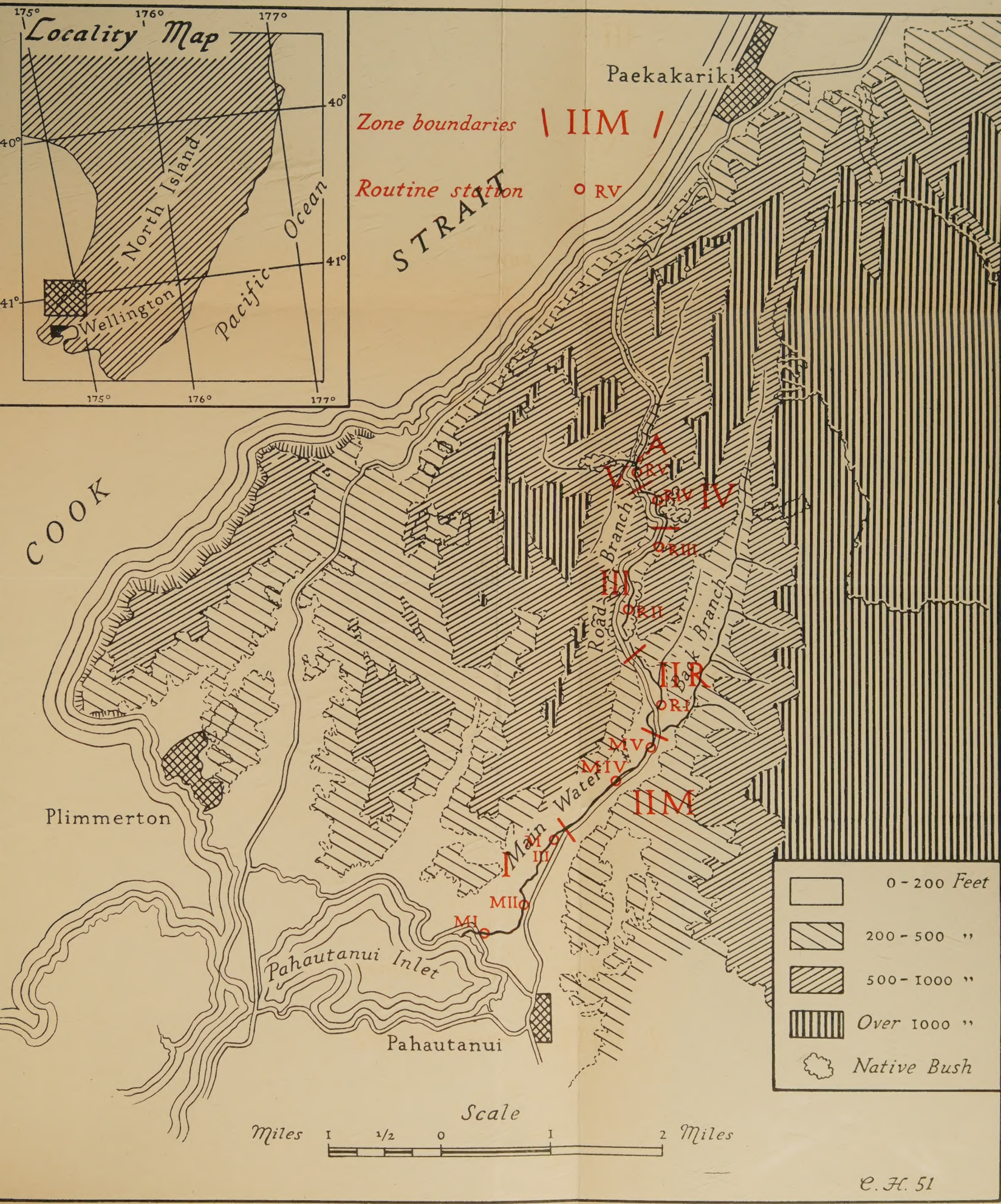
APPEND

ZONE

	Dec., 1939–Jan., 1940. Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	April, 1940. Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	June, 1940. Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	August, 1940. Mean Dry Wt.	Total Wet Wt.	We Wt. %
Hydropsyche	*1·20*	40·2	*13·9*	*1·42*	45·0	*9·1*	*2·06*	35·5	*10·7*	*2·18*	31·3	*6*
Rhyacophilidæ larvæ	*0·67*	9·4	*3·2*	*1·11*	8·0	*1·6*	*0·90*	10·5	*3·1*	*1·46*	27·6	*5*
„ pupæ	..	..	..	*2·62*	8·2	*1·6*	*2·62*	7·1	*2·1*	*2·62*	24·7	*5*
Helicopsyche	0·92	50·4	*17·3*	0·79	45·4	*9·1*	0·95	85·3	*25·2*	1·12	112·8	*24*
Olinga larvæ	*0·46*	2·6	*0·9*	*0·46*	8·1	*1·6*	*0·46*	8·1	*2·4*	*0·46*	15·4	*3*
Sericostomatidæ—												
Type " C " larvæ	0·37	9·3	*3·2*	0·19	3·1	*0·6*	0·36	10·5	*3·1*	0·32	6·4	*1*
„ pupæ	*1·61*	1·5	*0·5*	*1·61*	0·5	*0·1*	*1·61*	0·2	*0·1*	*1·61*	3·5	*0*
Pycnocentrodes larvæ	0·45	23·0	*7·9*	0·22	4·9	*1·0*	0·31	11·3	*3·3*	0·17	7·6	*1*
„ pupae	*4·81*	1·0	*0·3*	*4·81*	1·9	*0·4*	..	..	..	..	..	.
Coloburiscus	*2·27*	46·1	*15·9*	*0·83*	47·2	*9·5*	*1·32*	21·7	*6·4*	*0·66*	6·9	*1*
Deleatidium	0·37	38·8	*13·4*	0·41	201·5	*40·6*	0·28	93·2	*27·5*	0·31	126·9	*27*
Leptoperlidæ	*0·10*	0·2	*0·1*	*0·88*	4·2	*0·8*	*0·82*	3·3	*1·0*	*1·11*	6·6	*1*
Parnidæ imagines	*0·40*	0·7	*0·2*	..	..	..	*0·40*	0·1	*0·0*	..	..	.
„ larvæ	0·20	25·8	*8·9*	0·38	38·6	*7·8*	0·51	6·3	*1·9*	0·41	5·1	*1*
Chironomidæ larvæ	0·17	0·1	*0·1*	0·07	0·7	*0·1*	*0·05*	0·7	*0·2*	0·05	3·4	*0*
„ pupæ	..	..	..	0·07	0·6	*0·1*	*0·13*	0·4	*0·1*	*0·18*	3·5	*0*
Simuliidæ larvæ	..	..	..	..	..	..	*0·19*	0·2	*0·1*	*0·19*	0·2	*0*
„ pupæ	..	..	..	..	..	..	..	..	..	..	..	.
Other Diptera larvæ	*0·47*	1·8	*0·6*	0·54	2·3	*0·5*	*0·39*	1·9	*0·6*	*0·39*	5·7	*1*
Potamopyrgus	0·96	12·9	*4·4*	0·35	50·6	*10·2*	*0·25*	3·8	*1·1*	*0·13*	3·5	*0*
Latia	*2·06*	1·9	*0·7*	*0·45*	1·4	*0·3*	*0·11*	0·4	*0·1*	*0·25*	0·5	*0*
Oligochaeta	*5·53*	25·2	*8·6*	*5·53*	25·2	*5·1*	*5·53*	37·8	*11·1*	*5·53*	73·5	*15*
Total	..	290·9	*100·1*	..	497·4	*100·1*	..	338·4	*100·1*	..	465·1	*99*

X II

	October, 1940.			December, 1940.			February, 1941.			April, 1941.			October, 1941.		
	Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	Mean Dry Wt.	Total Wet Wt.	Wet Wt. %	Mean Dry Wt.	Total Wet Wt.	Wet Wt. %
7	*1·73*	25·5	*6·2*	*0·60*	13·0	*2·7*	*0·60*	11·9	*14·0*	*2·06*	48·1	*33·6*	*1·97*	17·0	*10·3*
9	*0·90*	12·1	*2·9*	*0·95*	18·4	*3·8*	0·45	1·6	*1·9*	*0·62*	3·4	*2·3*	*0·33*	0·6	*0·4*
3	*2·62*	23·5	*5·7*	*2·62*	18·8	*3·9*	..	..	..	..	..	..	..	..	..
3	1·61	155·6	*37·7*	3·15	170·8	*35·1*	0·89	28·7	*33·7*	0·21	13·9	*9·7*	0·73	21·3	*12·9*
3	*0·46*	10·6	*2·6*	*0·46*	8·7	*1·8*	*0·46*	0·1	*0·1*	*0·46*	0·2	*0·1*	*0·46*	1·1	*0·7*
4	0·80	10·6	*2·6*	0·64	6·3	*1·3*	0·19	2·6	*3·0*	0·18	5·4	*3·8*	0·88	8·4	*5·1*
7	*1·61*	11·1	*2·7*	*1·61*	4·8	*1·0*	*1·61*	3·4	*4·0*	*1·61*	2·5	*1·7*	..	..	..
6	0·40	18·9	*4·3*	0·64	24·3	*5·0*	0·17	0·4	*0·5*	0·25	2·5	*1·7*	0·45	6·2	3·8
	4·81	0·6	*0·1*	*4·81*	1·3	*0·3*	*4·81*	0·6	*0·7*	*4·81*	0·3	*0·2*	..	..	..
5	*3·23*	25·2	*6·1*	*1·77*	20·7	*4·3*	..	..	..	*1·01*	2·0	*1·4*	*3·28*	30·8	*18·7*
3	0·12	39·8	*9·6*	0·40	144·8	*29·8*	0·28	28·1	*32·9*	0·13	47·8	*33·4*	0·55	47·3	*28·7*
4	*0·58*	1·3	*0·3*	*0·38*	1·8	*0·4*	..	..	..	..	..	..	*0·58*	1·1	*0·7*
	0·40	0·1	*0·0*	*0·40*	0·7	*0·1*	*0·40*	0·2	*0·2*	*0·40*	0·2	*0·1*	..	..	..
1	0·25	10·7	*2·6*	0·28	14·3	*2·9*	*0·33*	2·8	*3·3*	*0·41*	6·5	*4·5*	*0·25*	5·3	*3·2*
7	0·06	1·3	*0·3*	0·03	1·2	*0·2*	0·06	0·2	*0·2*	*0·05*	1·1	*0·8*	*0·05*	0·4	*0·2*
8	*0·08*	0·5	*0·1*	*0·06*	0·4	*0·1*	..	..	..	..	..	..	..	..	..
0	*0·19*	0·2	*0·0*	*0·19*	0·1	*0·0*	..	..	..	..	..	..	..	..	..
	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
2	*0·24*	4·4	*1·1*	0·19	4·0	*0·8*	0·12	0·2	*0·2*	0·33	0·8	*0·5*	*0·24*	0·4	*0·2*
8	0·11	2·1	*0·5*	*0·13*	1·5	*0·3*	*0·33*	0·3	*0·3*	*0·06*	0·1	*0·1*	*0·10*	0·0	*0·0*
1	*0·06*	0·1	*0·0*	..	..	..	..	..	..	..	..	..	..	..	..
8	*5·53*	58·8	*14·2*	*5·53*	31·5	*6·5*	*5·53*	4·2	*4·9*	*5·53*	8·4	*5·9*	*5·53*	25·2	*15·3*
9	..	413·0	*96·6*	..	487·4	*100·3*	..	85·3	*99·9*	..	143·2	*99·8*		165·1	*100·2*


Locality Map
175°
176°
177°
40°
41°
North Island
Pacific Ocean
Wellington
Zone boundaries
Routine station
RV
STRAIT
Paekakariki
COOK
Plimmerton
Pahautanui Inlet
Pahautanui
Road Branch
Bak Branch
Main Water
A
V
IV
III
IIR
IIM
I
ORV
ORIV
ORIII
ORII
ORI
MV
MIV
MIII
MII
MI
0 - 200 Feet
200 - 500 "
500 - 1000 "
Over 1000 "
Native Bush
Scale
Miles 1 1/2 0 1 2 Miles
C. H. 51

Most of the trout needed in this work were caught by netting. Here the net is being worked up through a deep pool in the lower part of the Horokiwi.

[*Frontispiece*